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EAR AND TASSEL DEVELOPMENT IN MAIZE

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A study of the changes that take place in the growing points which form the ear and tassel of maize, or Indian corn, reveals a number of relationships that cannot be seen in the mature plant. It shows how the parts of the ear and tassel are formed from the growing point; where the parts are placed in relation to each other; and the sequence of the differentiation of the parts. Such a study is focused on the beginning rather than on the end of the developmental cycle and as a consequence a better understanding can be attained of variations in certain characteristics such as ear row number, ear height, time of sexual maturity, and of certain correlations in the development of the tassel and ear.

This paper will be limited to a description of the differentiation and development of the ear and tassel of the corn plant. Normal development will be emphasized; however, a description of certain abnormal ear types will be included. Part of the photomicrographs were published earlier (Bonnett, 1940) and are used again in this paper because they show clearly the various developmental stages of the ear and tassel and their parts. The descriptions of these illustrations have been revised.

LITERATURE REVIEW

Certain authors have made extensive reviews of the literature on the morphology of corn and other grasses. Literature on the general morphology of the corn plant has been reviewed by Weatherwax (1916, 1917, 1925), Miller (1919), Arber (1934), and Randolph (1936). Evans and Grover (1940) have a good literature review on the morphology of grasses.

The general morphology of the tassel and ear of the corn plant has been described by Collins (1919), Weatherwax (1916, 1917, 1925), and Arber (1934). Pistillate spikelet development was clearly described by Miller (1919). Randolph (1936) described the development of the caryopsis as well as the pistillate spikelet.

Few studies of the early stages in the development of the ear and tassel of corn have been published. Noguchi (1929) described some of the beginning stages in the development of the ear and tassel. Development of the ear and certain of its characteristics were described by Fujita (1939). A detailed description of the development of the ear and tassel, illustrated by photomicrographs, was published by Bonnett (1940).

Publications dealing with corn morphology from certain specific viewpoints should also be mentioned. A paper by Anderson (1944) on the homologies of the ear and tassel is of value to both the corn breeder and the student of corn morphology. Mangelsdorf has brought together the pertinent information on the morphology of the ear as it is related to the question of the origin and nature of the corn ear. A paper by Cutler (1946) and one by Brown and Anderson (1947) describe morphological details of the ear and tassel of special types of corn.

MATERIALS AND METHODS

First-generation hybrid plants, Golden Cross Bantam (Purdue Bantam 39 × Purdue 51) and a Country Gentleman hybrid (Illinois 8 × Illinois 6) sweet corn, were used in working out the details of tassel and ear development. Plants of first-generation hybrids are genetically alike and variation among individual plants is slight, which makes it easier to follow the developmental sequences. The sweet corn plants were grown in the greenhouse in two-gallon jars. Plants of the other ear types were grown in the field.

Seed of the various ear types was obtained from different sources. The Maize Genetics Cooperation, Cornell University, Ithaca, N. Y., furnished seed of 4-row and ramosa. Seed of Longfellow flint and Japanese Hull-less came from William L. Brown, Pioneer Hi-Bred Corn Company, Johnston, Ia. R. R. St. John, DeKalb Hybrid Seed Company, Champaign, Ill., supplied seed of Mexican Long Kernel.

Most of the photomicrographs were taken of living material which was handled as was described by Bonnett (1940). However, tassels and ears of the different ear types were killed and fixed in a formalin—acetic acid—alcohol solution and later dissected and photographed.

PLANT DEVELOPMENT

The beginning of the differentiation of the tassel can be approximately determined by counting the number of leaves or by examining the base of the plant to see if internode elongation has begun (pl. 31). Leaf number is less reliable owing to the fact that early types have fewer leaves than late ones at the time tassel differentiation begins and to the effect of the environment upon the relation between leaf number and tassel differentiation. Beginning of internode elongation has been found to be associated with the beginning of tassel differentiation (pl. 31). However, when it can be determined from an external examination of the plant that the basal internodes are elongating, the earliest stages of tassel development have usually been completed. The only reliable method of determining when tassel development begins is to dissect the growing point of the main shoot and

look at it with a dissecting microscope. If sampling begins early enough and is done at frequent intervals the beginning of tassel development can be accurately determined.

Initiation of ear development is behind the initiation of tassel differentiation. Silking may be synchronized with shedding or it may be ahead of or after pollen shedding on the same plant. Silking date and its synchronization with pollen shedding varies with the variety and with growing conditions.

TASSEL AND STAMINATE SPIKELET DEVELOPMENT

The shoot of the corn plant, like that of other cereals (Bonnett, 1935, 1936, 1937, 1940) and grasses (Evans and Grover, 1940; and Weber, 1938, 1939), passes through two stages in its development from germination to the dehiscence of the anthers. During the first stage, leaf fundaments, leaves, and axillary shoots are produced and the internodes of the stem remain short. During the second stage the internodes of the stem elongate, the tassel and its parts differentiate and develop, and the axillary shoot or shoots (ear or sucker) pass through their various stages of development.

Two growing points (pl. 24, A and B) represent the appearance of the shoot in the first stage of development. The growing point (pl. 24, A, *gp*) is partly enclosed by two leaf initials. At this stage of development the growing point is much smaller in relation to the diameter of the stem than the growing point of either wheat, oats, or barley at a similar stage of development.

Two processes, which occur simultaneously, indicate the beginning of the second stage of development: (1) The internodes of the stem begin to elongate, and (2) the growing point elongates in preparation for the differentiation of the tassel and its parts. Tassel development is completed when the anthers dehisce.

Branch primordia are the first of the tassel parts to differentiate (pl. 24, C, *b*, and D, *b*). They arise in acropetal succession as lateral projections from all sides of the elongated central axis. Some of the branch initials at the base of the central axis elongate and become the lateral axes of the tassel (pl. 24, E, b_1). The other initials arising from a point higher on the central axis are the ones from which the spikelet initials originate (pl. 24, C, *b;* D, *b;* E, *b;* F, *si;* and G, *si*). It should be noted that, in the early stages of tassel development, so far as external appearances indicate, there are no differences between those initials that become the lateral branches of the first order and those from which the spikelet initials differentiate. Therefore, all of the first initials to appear are branch initials.

As has been described for oats (Bonnett, 1937) and grasses (Evans and Grover, 1940), branches of the second order may rise by budding from the base, and at the lateral margins, of the branches of the first order (pl. 24, E, b_2, and K, b_2). It has already been stated for the central axis that those initials of the lateral axes above the most basal ones are the primordia from which the spikelet initials differentiate.

In studies made on barley, wheat, and oats (Bonnett, 1935, 1936, 1937) and grasses (Evans and Grover, 1940), there was always an indication of leaf fundaments on the central axis in the axils of which the lateral shoots of the inflorescence were formed. Although there is no indication of leaf fundaments subtending the initials of the lateral shoots of the tassel of the sweet corn studied, in certain other types of corn they have been found. There are structures apparently homologous with leaf initials, subtending the lateral shoots of the ear (pl. 26, C, *l*).

All the branches of the tassel are indeterminate. Neither the central axis (pl. 24, I, *t*) nor the lateral axes (pl. 24, J, *t*, and K, *t*) of the tassel terminate in apical spikelets. Primordia from which the spikelet initials differentiate are produced acropetally as long as the axes increase in length.

In the beginning of spikelet development the branch initial divides into two unequal parts, the spikelet initials (pl. 24, F, *si;* G, *si;* and H, *si*). The spikelet that develops from the larger spikelet initial is pediceled (pl. 25, E, *s'*) and the one from the smaller initial is sessile (pl. 25, E, *s*). The larger initial is always in advance of the smaller in its development. This is shown by the beginning of development of the empty glume on the larger initial in plate 24, H, *e*, and the lack of such development in the smaller initial, and by the beginning of anther differentiation in the larger spikelet in plate 25, C, *s'*, and the lack of anthers in the smaller spikelet (pl. 25, C, *s*).

Several of the early stages of spikelet development can be seen in plate 24, H, which shows a group of spikelets from the central axis of the tassel. Beginning at the top of the photograph, the developmental stages range from an undifferentiated lateral shoot initial, through the various stages of division into spikelet initials, to the beginning of development of the empty glumes. The empty glumes are the first of the spikelet parts to form and are first seen as transverse ridges across the spikelet initial (pl. 24, H, *e*). They grow in length and finally enclose the flowers (pl. 25, I). Spikelet initials develop from all sides of the central axis of the tassel (pl. 24, G) but only on the abaxial side of the lateral branches. The abaxial side of branches of the first and second order are shown in plate 24, K, b_1, b_2, and the adaxial side of a branch is shown in plate 24, J. Two rows of lateral shoot primordia develop, and they divide into two pairs of spikelet initials.

At any stage of development the central axis of the tassel is in advance of the branches (pl. 24, F, L, and M). This is what should be expected since the central axis is formed first and the branches differentiate from it. The branches increase considerably in size before the initials from which the spikelets differentiate are produced.

In each staminate spikelet two flowers develop from the meristem located above the empty glume initials (pl. 24, H, *gp'*). The meristem divides into two unequal parts. The larger part gives rise to the upper flower (pl. 25, A, fl_1, and B, fl_1) and the smaller part develops into the lower flower (pl. 25, A, fl_2, and B, fl_2). These flowers differ in their rates of development. The anthers of the upper flower (pl. 25, A, fl_1; B, fl_1; D, fl_1; and G, fl_1) differentiate first, and

their development is always ahead of the corresponding parts of the lower flower (pl. 25, A, fl_2; B, fl_2; D, fl_2; and G, fl_2). As the flowers approach maturity the anthers of the lower flower attain nearly the same size as those of the upper flower (pl. 25, G, fl_1, and fl_2).

Anther initials are the first of the flower parts to differentiate (pl. 25, A, *an*, and B, *an*). Since the tassel flowers are staminate, anther differentiation and development are the principal growth activities within the flower. Pistils may develop from the meristem located above the anther initials (pl. 25, A, *p*) but they usually remain rudimentary (pl. 25, B, *p*). Under certain conditions of growth the pistil may show considerable development (pl. 25, F, *p*) and may become fully developed and functional. Flowering glumes develop for each flower, but they are so thin (pl. 25, G, *g*) that they are difficult to distinguish at the beginning of their development. The lemma and palea begin their development as thin ridges at a point on the meristem just below the anther initials (pl. 25, B, *g*) at about the same time that the anther initials begin to differentiate.

Deviations from the normal development under field conditions are often seen in plants grown in the greenhouse. Normally one spikelet is sessile and the other pediceled (pl. 25, E), but both spikelets may be sessile (pl. 25, H). Another type of deviation which will be described later is the development of functional pistils in the tassel.

EAR AND PISTILLATE SPIKELET DEVELOPMENT

In the early stages of stem development a shoot is produced in the axil of each leaf, but at a later stage axillary shoots are no longer produced. The cessation of axillary shoot development seems to be associated with the elongation of the internodes of the stem and the development of the tassel.

Ears develop from the upper one or more axillary shoots of the stem. Those shoots, formed at the base of the stem, may remain non-functional or develop into suckers. If an examination is made at the time the topmost shoots are producing ear initials, it will be found that the growing points of the basal shoots are producing only leaf fundaments; but they are more and more advanced in development from the base to the top of the stem. Axillary shoots develop in acropetal succession and during the early stage of stem development they become larger in succession from the apex to the base of the stem. Later, when the ears begin to develop, the size sequence changes, so that the topmost shoot is the largest and the shoots become smaller from the top to the base of the plant. The topmost shoot or the topmost two or three shoots, depending upon whether they are single- or multiple-eared types, in turn take precedence in their development or they may inhibit the development of the shoot immediately below. This difference in development is shown by the size of the ear initials in plate 26, I, J, and K, which are the ear initials from the topmost, second, and third shoots, respectively. The axillary shoot is enclosed in a strongly keeled prophyllum (pl. 26, A, *pr*, and B, *pr*) which may be entire or divided. Leaf initials that develop into husks are covered by the prophyllum.

Ear differentiation is indicated by an elongation of the growing point of the axillary shoot and the differentiation of lateral projections from the central axis of the ear initial (pl. 26, C, and D). The lateral projections are the branch initials from which the spikelet initials differentiate, and correspond to the branch initials that first appear on the central axis and branches of the tassel. Subtending each initial, as has already been mentioned, are ridges (pl. 26, C, *l*) which are similar to the subtending leaf initials that appear in the differentiation of the inflorescences of barley, oats, and wheat. These ridges increase in size and form the cup-like depressions (alveoli) in which the spikelets occur (pl. 28, B, *x*).

Spikelet initials are produced in pairs by the division of the preceding initial into two unequal parts (pl. 26, E, *si*). Thus in the ear there is potentially a pediceled and a sessile spikelet from each branch initial, as in the tassel, although the subsequent development of the spikelets do not seem to bear this out. While the parts of the larger of the pair of spikelet initials begin to differentiate before those of the smaller spikelet initial, the difference in their development is not so great as was pointed out for the spikelet initials of the tassel. The empty glumes are the first of the spikelet parts to form and can be seen as transverse ridges across the spikelet initial (pl. 26, F, *e*, and pl. 27, A, *e*). More advanced stages of development of the glumes are shown in plate 26, G, *e*. As the empty glumes increase in length, they enclose the ovary, but the silk extends beyond them (pl. 27, K, *e*).

The number of rows of kernels per ear is determined by the number of rows of branch initials that differentiate. Each branch initial divides into two spikelet initials and each spikelet initial has one fertile flower in which a kernel is produced. This pattern of development results in an even number of rows of kernels. However, row number is actually determined by the number of rows of branch initials (pl. 26, E) that are produced on the ear initial.

Straightness of the rows of kernels has been shown to be related to the number of rows of branch initials on the ear (Fujita, 1939). If the number of rows of branch initials is even, 4, 6, 8, etc., resulting in 8, 12, 16, etc. rows of kernels, the rows will be straight, making a balanced, symmetrical ear (Mangelsdorf, 1945). If the number of branch initials is odd, 3, 5, 7, etc., resulting in 6, 10, 14, etc. rows of kernels, the rows will be twisted, making an unbalanced, asymmetrical ear. Mangelsdorf (1945) has pointed out that this relationship applies to North American and other varieties of corn which have *Tripsacum* contamination but in Bolivian and Peruvian corn, the twisted-row character is usually independent of row number.

The ear, as well as the tassel, is indeterminate in its growth and continues to elongate at the tip (pl. 26, H, *t*), but many of the flowers at the tip of the ear remain rudimentary (pl. 28, C, *t*). Since the spikelets arise in acropetal succession they are successively younger from the base to the tip of the ear (pl. 26, G and H).

Two flower initials are produced in each spikelet, but in most corn varieties only one flower is functional. In a few types like Country Gentleman sweet corn both flowers are functional.

The two flowers of the ear develop from an unequal division of the meristem of the spikelet just as was pointed out for the flowers of the tassel. The flower differentiating from the larger mass of meristem (the upper flower) takes precedence in its development over the one from the smaller mass of meristem (the lower flower). The larger flower is the functional flower in those types of corn that have only one functional pistillate flower per spikelet. In the types of corn having two functional pistillate flowers per spikelet, the larger flower is more advanced at every stage in its development than the smaller flower.

Anther initials are the first of the reproductive parts of the flower to differentiate (pl. 27, B, *an*). In the pistillate flower the anthers begin differentiation but usually remain small and non-functional. Under certain growth conditions and in the genetic-type anther ear, the anthers of the pistillate flower may attain full development. Anthers well enough developed to show the locules are shown in plate 27, G, *an*, and J, *an*.

The pistil initial develops from the apex of the growing point which is located between the anther initials (pl. 27, B, *p*, and I, *p*). Development begins with the formation of a ridge, the silk initial, which partly encircles the tip of the growing point (pl. 27, C, *s*, and D, *s*). The ovule differentiates from the meristem which is partly enclosed by the developing silk initial (pl. 27, C, *ov*, and E, *ov*). The margin of the silk initial grows more rapidly on one side than on the other (pl. 27, E, *s*). Soon two distinct points appear (pl. 27, F and G) which continue to elongate (pl. 27, G and K) and which finally result in the biparted tip of the mature silk (pl. 28, E). Unequal growth rates of the margins of the silk initial result in the development of a tube-like structure partly enclosing the ovule (pl. 27, E, *ov*). The opening above the ovule gradually closes and becomes the stylar canal (pl. 27, G, *sc;* H, *sc;* and K, *sc*). As the silk elongates it becomes covered with hairs, the structure of which has been described by Weatherwax (1917) and Miller (1919). Hairs are just beginning to appear as fine points upon the silk in plate 27, K, *s*, and L, *s*, and they are shown, fully developed, with pollen grains germinating upon them, in plate 28, E, F, and G. The ovary is shown in plate 28, D, *o*, with the silk attached and partly enclosed by the flowering glumes. At this stage of pistil development all of the external parts have differentiated but the pistil has not attained full size. Silks begin to develop first at the base of the ear (pl. 28, A), and at the later stages of ear development a marked contrast in the length of the silks at the tip and the base of the ear can be seen (pl. 28, C).

An enlargement of a section of the ear at the same stage of development as in plate 28, A, is shown in plate 28, B, in which the attachment of the spikelets, variation in the length of the silks, and the size of the stylar canal can all be seen.

Very soon after pollen grains lodge upon the silk they germinate, and the pollen tube grows down the hair into the silk (pl. 28, F and G). This process has been described by Miller (1919) and Randolph (1936).

DEVIATIONS FROM NORMAL FLOWER DEVELOPMENT

Two deviations from normal flower development will be illustrated and described. The first is the development of two fertile flowers in a pistillate spikelet and the second is the development of pistillate spikelets in the tassel. Illustrations for the first deviation were taken from Country Gentleman sweet corn and are shown in plate 27, I, J, L, and M. Illustrations for the second deviation were taken from Golden Cross Bantam and are shown in plate 29.

It will be recalled that in those types of corn that have only one fertile flower per spikelet, the sterile flower begins but does not complete its development. The sterile flower develops from the smaller of the two divisions of the growing point of the spikelet initial. Anther initials and the pistil initial of the sterile flower differentiate (pl. 27, G, fl_2) but do not complete their development (pl. 27, H, fl_2). The pistil of the fertile flower develops as has been described, but the anthers do not, so that in examining a spikelet of the ear of those types of corn having one fertile flower per spikelet, all that can be seen after the silk has begun to elongate are the empty glumes (pl. 27, K, *e*) and the silk of the fertile flower extending beyond them (pl. 27, K, *s*).

When two fertile flowers develop in a pistillate spikelet each flower goes through the same sequence of development that has been described, but the rates of development are different. The upper flower arising from the larger of the two divisions of the growing point develops more rapidly than the lower flower. This was also pointed out for the development of the two flowers of the spikelet in the tassel. The differences in rates of development of the upper and lower flowers can be seen by comparing the upper flower in plate 27 (I, fl_1; J, fl_1; L, fl_1; and M, fl_1), with the lower flower (fl_2). While the upper flower develops first, the lower flower gradually overtakes the upper flower as the ear approaches maturity, but a difference in the development of the silks persists so that the silks of the two flowers do not emerge at the same time.

Paired grains of corn result when two fertile flowers are produced per spikelet. The germ of the upper flower faces the tip of the ear and the germ of the lower flower faces the base of the ear, resulting in the kernels being placed back to back. With the development of two grains per spikelet the kernels may be crowded out of line so that there are irregular rows or a lack of rows as shown in Country Gentleman sweet corn. Development of paired grains, according to Randolph (1936), was first described in pod corn by Sturtevant (1894), and Kempton (1913) was the first to interpret correctly the development of paired grains as being the result of the development of two fertile flowers per spikelet. Weatherwax (1925), Stratton (1923), and others have also described the development of double kernels.

The development of pistillate spikelets in the tassel is an interesting deviation from normal development. Kempton (1913) has pointed out that if there are pistillate flowers in the staminate inflorescence, it is the upper flower of the sessile

spikelet that is pistillate and both of the flowers of the pediceled spikelet are staminate (pl. 29, A). Spikelet differentiation and the first stages in the development of the flowers are the same in both the staminate and the pistillate spikelets of the tassel. The essential difference lies in the degree of development of the anthers and pistils. In the pistillate flowers both the anthers and the pistil differentiate but the pistil takes precedence in development; in the staminate flowers both the anthers and pistil differentiate but the anthers develop instead of the pistil.

In most corn varieties only one flower, the upper one, of the spikelets of the ear is fertile, and the same is true of the pistillate spikelet produced in the tassel (pl. 29, B). Consistent with the development of the flowers of the ear of this type, the upper flower (pl. 29, A, fl_1, and C, fl_1) developed and the lower flower was abortive (pl. 29, A, fl_2, and C, fl_2). Pistil differentiation and development were the same as previously described for the pistillate flower of the ear. The various stages in the development of the silk are shown in plate 29, A, *s*, to F, *s*, inclusive, and it can be seen that they are essentially the same as already described.

The development of the flowers of the staminate spikelet shows no deviation from normal development except that the pistil is a little further developed than in the tassels having only staminate spikelets. But the example shown in plate 29, A, *x*, should not, perhaps, be considered as typical because even in those plants that did not have pistillate spikelets, a considerably greater degree of pistil development was noted (pl. 25, F, *p*, and H, *p*) than would be expected in plants grown in the field. However, this is what should be expected of corn plants grown in the greenhouse under certain conditions of temperature and light.

EAR TYPES

Tassels and ears of four different ear types at early stages in their development are shown in plate 30. They are: four-row, Longfellow flint, ramosa or branched ear, and fasciated. These ear types are of interest because they deviate from the normal ear type of commercial corn.

In corn with four-rowed ears the spikelets on the central axis of the tassel and on the ear are in two ranks (pl. 30, D and H). The tissue between the ranks of spikelets develops into the cob. Ears of the four-rowed type used in this study varied (pl. 30, E) in the number of rows of spikelets per rank and sometimes there was a mixture of two and three rows of spikelets in the same rank. Some of the four-rowed plants developed four ranks of spikelets. They were eight-rowed like Longfellow flint.

The spikelets on the ear and central axis of the tassel of Longfellow flint are in four ranks (pl. 30, A, B). This gives the ear or tassel, in its early stages of development, the appearance of being square. The ear and central axis of the tassel are long, slender, and sharply pointed at the tip. The four-ranked appearance of the central axis of the tassel and of the ear is the result of the position of the spikelets (Brown and Anderson, 1947). In the tassel there are two pairs of spikelets opposite each other at a node. At any node the spikelets are at right

angles to the spikelets immediately below and immediately above and this arrangement gives the four-ranked appearance.

A ramosa ear resembles a tassel in all of its morphological characteristics (pl. 30, I, J). It has a central axis and lateral branches arising from it. Collins (1917) has described how the ramosa tassel differs from that of normal corn, as follows: "In the Z. *ramosa* tassel the branches are more numerous and gradually decrease in size from the base upward, the transition from branches to pairs of spikelets being imperceptibly gradual." The same is true for the ear as can be seen in plate 30, I and J. In Z. *ramosa* the homology between the ear and tassel can be clearly seen because of the branching of both of the inflorescences. In normal corn, branching in the ear is suppressed but the tassel branches and therefore the ear and the tassel do not appear to be homologous.

Two fasciated types are shown in plate 30, Japanese Hull-less, and Mexican Long Kernel. At this stage of development, the ear and central axis of the tassel are short, thick, and blunt at the tip (pl. 30, C, F, and G). The similarity in the form of the central axis of the tassel and ear is clearly seen at this stage of development of Japanese Hull-less. The Mexican Long Kernel ear has a triparted tip. Other types of fasciated ears may be bi-parted, hollowed out, or flattened at the tip.

Anderson (1944) pointed out the correlation between condensation of the spikelets in the basalmost branch of the tassel and row number of the ear. He also stated that there is a correlation between the portion of the tassel branch that is condensed and the type of fasciation in the ear and the part of the ear that will be fasciated. The tassel of Japanese Hull-less illustrated here is too young to show this correlation. Older tassels of other fasciated types have been studied and they do show condensation of the spikelets. At very early stages of tassel and ear development the short, thick, blunt axis is a good indication of fasciation, and also of a high kernel row number.

SUMMARY

1. The developmental morphology of the tassel, ear, and their parts was studied by dissecting them from the corn plant at different stages in their development. Photomicrographs were taken of the various stages.
2. From germination to the dehiscence of the anthers, the shoot of the corn plant passes through two stages of development. In the first stage, leaves and axillary shoots are produced and the growing points of the main stem and axillary shoots remain short and shaped like a half sphere. In the second stage the growing points of the shoots and the internodes elongate and the tassel, ear, and their parts differentiate and develop.
3. Tassel and ear differentiation begins with the appearance of lateral projections, branch initials, which arise acropetally from the growing points. The branch initials at the base of the tassel elongate but the remainder on the central axis of the tassel and those which arise on the tassel branches differentiate into spikelet initials. All the branch initials of the ear of normal corn remain short

and differentiate into spikelet initials. Ramosa ear behaves like a tassel.

4. In both the tassel and ear the spikelet-forming branch initials divide into two unequal parts to form the spikelet initials which in turn divide into two unequal parts to form the flower initials. In the tassel the spikelet developing from the larger initial is pediceled and is ahead in development of the spikelet developing from the smaller initial, which is sessile. Likewise, the upper flower developing from the larger division of the pistillate spikelet is ahead of and larger than the lower flower developing from the smaller division of the pistillate spikelet.
5. In the ear the difference in the size of the spikelets arising from the unequal division of the branch initial is not so marked as in the tassel. The flower developing from the larger, upper division of the spikelet is the fertile flower, and the smaller, lower division is the abortive flower in those types of corn having only one fertile flower per spikelet. In those types of corn having two fertile flowers per spikelet the upper flower is larger and ahead of the lower flower in development.
6. Flower parts differentiate in the following order: empty glumes, flowering glumes, anthers, and pistil. In the pistil the order of development is ovary, silk, and hairs on the silk.
7. Four-row, ramosa, and fasciated are ear types that differ from the normal, and each type is described.

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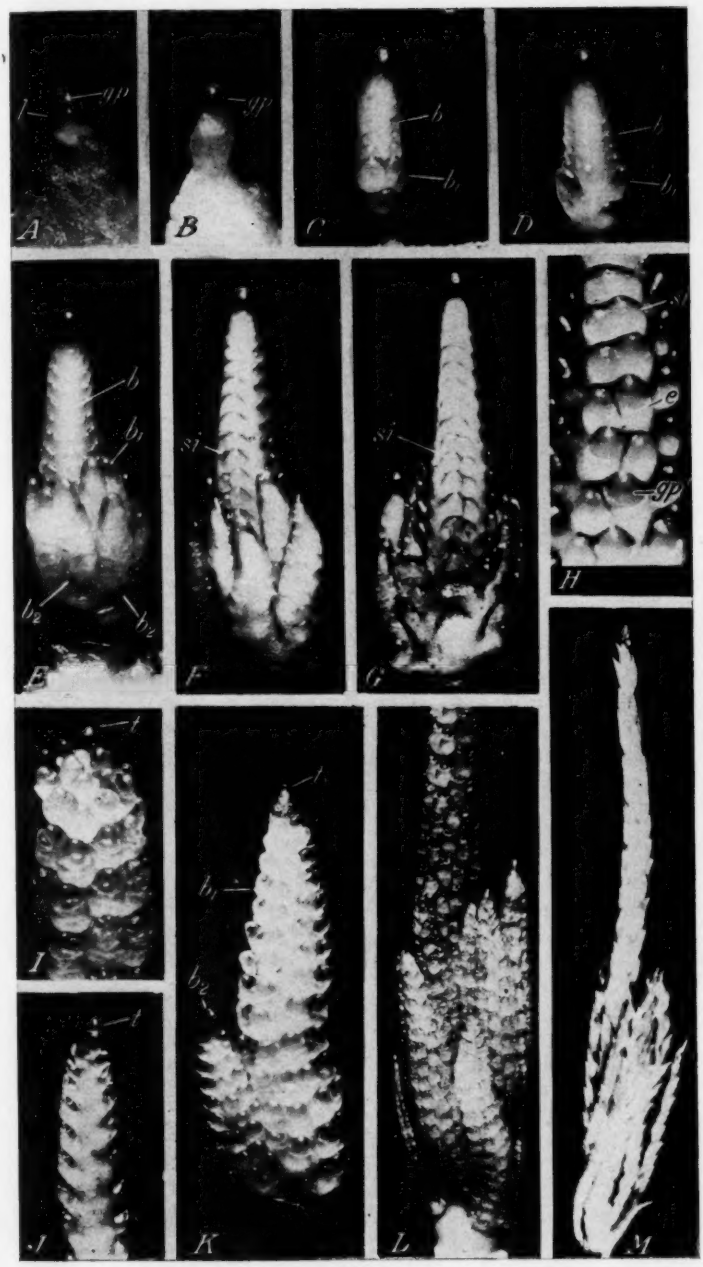
Explanation of Plate

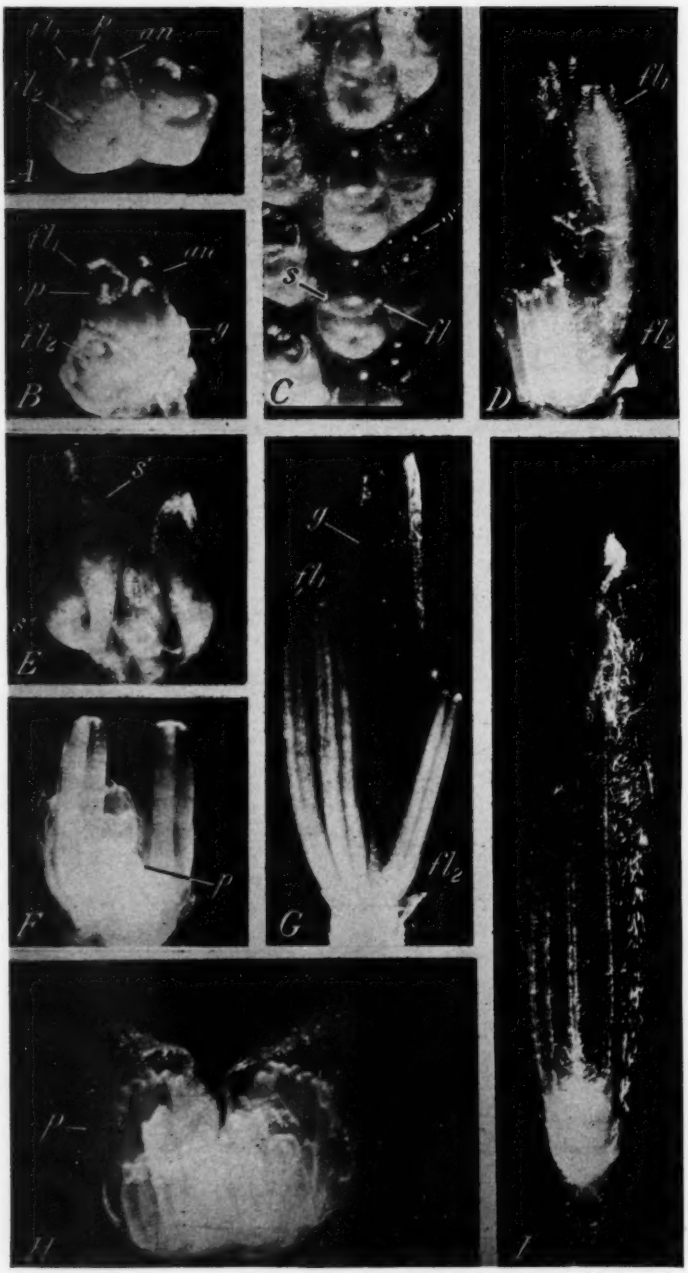
PLATE 24

Showing initiation and development of the tassel: *b*, branch initial from which spikelets differentiate; b_1, basal branch of the first order; b_2, branch of the second order; *e*, empty glumes; *gp*, growing point; *gp'*, growing point of the spikelet; *l*, leaf initial; *si*, spikelet initial; *t*, undifferentiated tip of an axis.

A—Growing point of a corn plant having four leaves visible, × 22.
B—Beginning of the elongation of the growing point just before tassel differentiation, × 22.
C and D—Differentiation of the branch initials of the tassel, × 22.
E—Elongation of the basal branches of the tassel, × 22.
F—Beginning of the differentiation of the spikelet initials on the central axis of the tassel, × 22.
G—A stage similar to F with some of the basal branches removed to show spikelet differentiation on the central axis, × 22.
H—Differentiation of spikelets and empty glumes on a portion of the central axis of the tassel, × 35.
I —Portion of the tip of the central axis of the tassel, × 25.
J —Adaxial side of a branch of the tassel, × 22.
K—Abaxial side of tassel branches of the first and second orders, × 25.
L—A more advanced stage of tassel development, × 22.
M—Fully differentiated but not full-sized tassel, × 8.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 25

All figures represent spikelet development in the tassel: *an*, anther; *fl*, flower initial; fl_1, upper flower; fl_2, lower flower; *g*, palea; *p*, pistil; *s*, sessile spikelet; *s'*, pediceled spikelet.

A—A pair of spikelets of the tassel at the beginning of the development of the flower parts. The upper flower, fl_1, is more advanced than fl_2, and the spikelet on the left, pediceled spikelet, is more advanced than the spikelet on the right, sessile spikelet, × 56.

B—Two flowers of a spikelet of the tassel showing the more advanced stage of the upper flower, fl_1.

C—Part of a branch of the tassel showing a more advanced stage of development of the pediceled spikelet, × 40.

D—Staminate spikelet with the empty glumes removed to show the difference in the size of the anthers of the upper and lower flower, × 20.

E—Two pairs of spikelets—one member of each pair is pediceled and the other sessile; the empty glumes have been removed from one spikelet, × 25.

F—Staminate flower with one anther removed to show the partly developed pistil, × 20.

G—Later stage of spikelet development in which the anthers of the lower flower are approaching the size of those of the upper flower, × 10.

H—A pair of spikelets both sessile, × 28.

I—A fully differentiated spikelet, × 10.

Explanation of Plate

PLATE 26

Development of the ear: *b*, branch initial from which spikelet initials differentiate; *e*, empty glumes; *l*, leaf fundament; *pr*, prophyllum; *si*, spikelet initial; *s*, silk initial; *t*, undifferentiated tip of the ear.

A—Axillary shoot in which the ear develops, enclosed in the prophyllum, × 13.

B—Side view of the axillary shoot, × 17.

C—Beginning of the differentiation of the ear, × 25.

D—A more-advanced stage of ear development showing the formation of branch initials, × 25.

E—Beginning of spikelet differentiation by an unequal division of the branch initials, × 22.

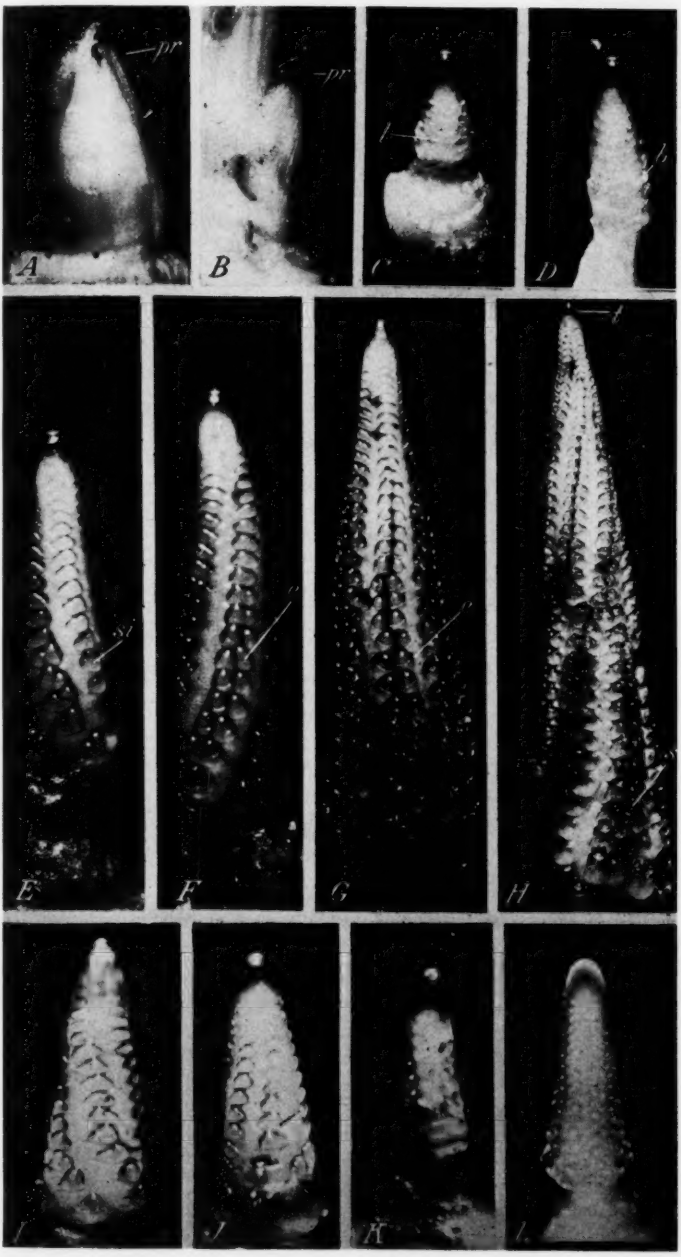
F—Development of the empty glumes as ridges on the growing point, × 22.

G—Paired rows of spikelets of the ear and, a more advanced stage, the development of the empty glumes, × 17.

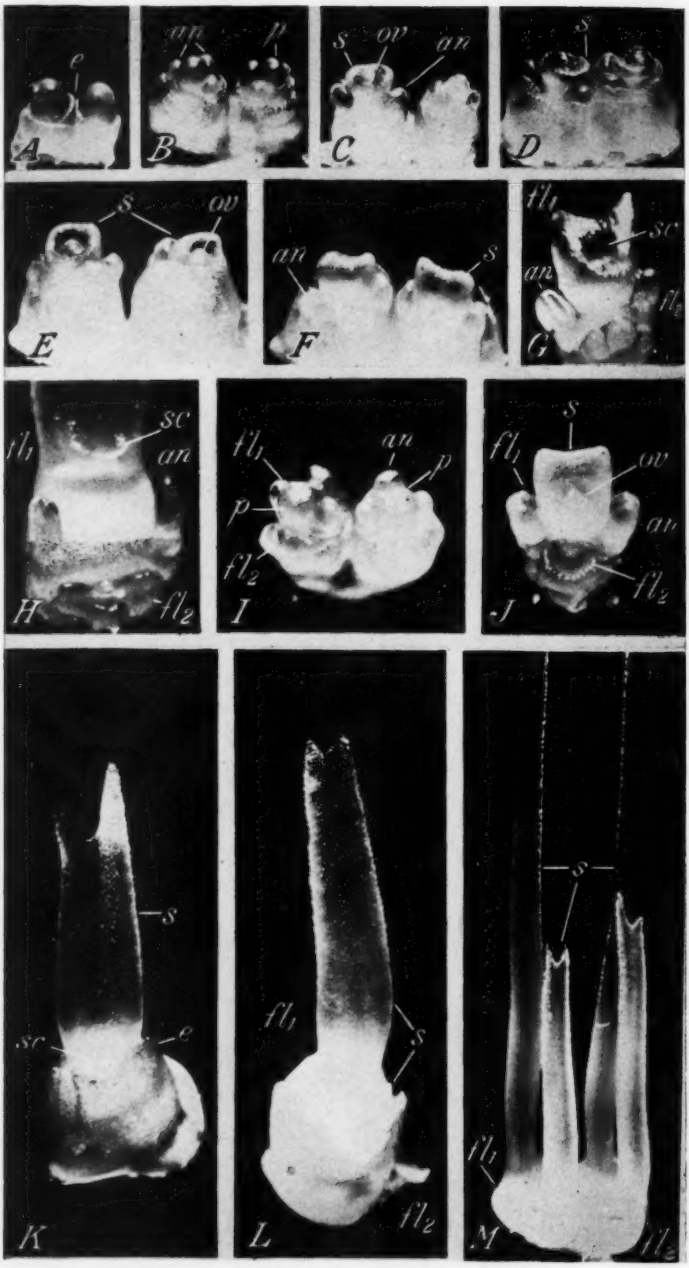
H—The differentiation and development of the silks can be seen at the base of the ear and an irregularity in the rows half way between the tip and butt, × 17.

I, J, and K—Topmost, second and third ears, respectively. All × 22.

L—Young ear of Country Gentleman sweet corn, × 17.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 27

Differentiation of the pistillate spikelet: *an*, anther initial; *e*, empty glumes; fl_1, upper flower; fl_2, lower flower; *ov*, ovule; *p*, pistil initial; *s*, silk initial; *sc*, stylar canal.

A—Pair of pistillate spikelets at an early stage of development, × 40.

B—Beginning of the differentiation of anthers in the upper flower of a pair of spikelets, × 40.

C—Differentiation of a silk, the first stage of pistil development, × 40.

D—Silk development, × 40.

E—Silks partly enclosing the ovules, × 40.

F—Silk development from the adaxial side, × 40.

G—Spikelet showing the comparative development of the upper and lower flowers, × 40.

H—Functional upper flower and sterile lower flower of a spikelet are illustrated, × 40.

I—Pair of spikelets of Country Gentleman; both flowers are functional, × 40.

J—Spikelet of Country Gentleman; the development of the upper flower is in advance of the lower flower, × 40.

K—Silk development of the functional flower of a spikelet having only one functional flower, × 28.

L—Comparison of the silk development of the lower and upper flowers of a spikelet having two functional flowers, × 28.

M—A more-advanced stage in the development of spikelets having two functional flowers, × 28.

Explanation of Plate

PLATE 28

A—Ear showing different stages of silk development, × 6.5.

B—Section of an ear showing silks at early stages of development and the ridge subtending each spikelet, × 19.

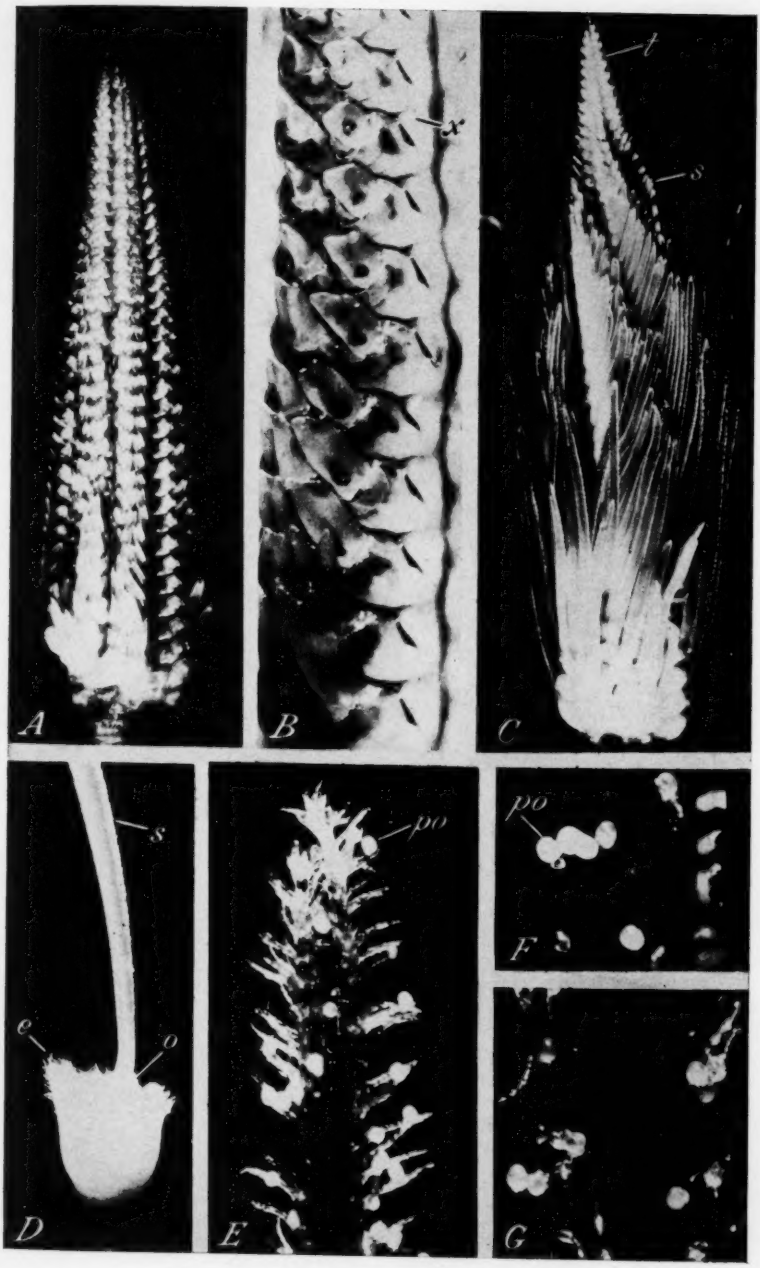
C—Variation in silk development from base to tip of ear, × 6.5.

D—Pistillate spikelet from a tassel, × 14.

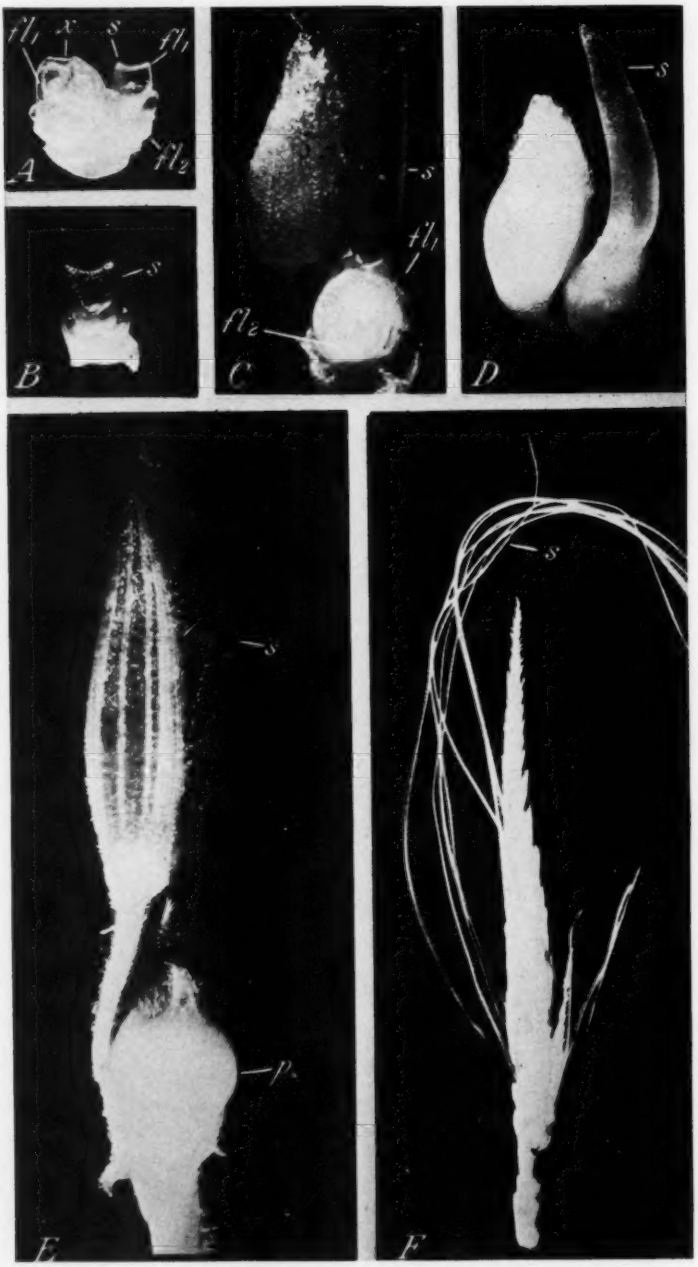
E—Tip of a mature silk with pollen grains germinating on it, × 26.

F and G—Pollen grains germinating on the silk, × 38.

e, empty glumes; *o*, ovary; *po*, pollen grain; *s*, silk; *t*, tip of ear; *x*, ridge subtending the spikelets of the ear.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 29

A—A staminate (left) and pistillate (right) spikelet from the tassel, × 20.

B—Silk development in a pistillate spikelet from the tassel, × 28.

C—Glumes removed from the pistillate spikelet to show the abortive lower flower, × 20.

D—Staminate and pistillate spikelets of the tassel, × 15.

E—A fully differentiated staminate, pediceled, and pistillate, sessile, spikelet of the tassel, × 10.

F—A tassel showing silks from the pistillate spikelets at the base of the tassel, × 10.

fl_1, upper flower; fl_2, lower flower; *p*, pistil; *s*, silk; *x*, upper flower of the staminate spikelet.

Explanation of Plate

PLATE 30

A—Tassel of Longfellow flint showing the development of spikelets on the central axis.

B—Ear of Longfellow flint. The arrangement of its eight rows of spikelets gives it the appearance of being square.

C—Ear of fasciated type, American Long Kernel. The tip of the ear is triparted.

D—Tassel of four-rowed corn. The spikelets on the central axis of the tassel are in two ranks.

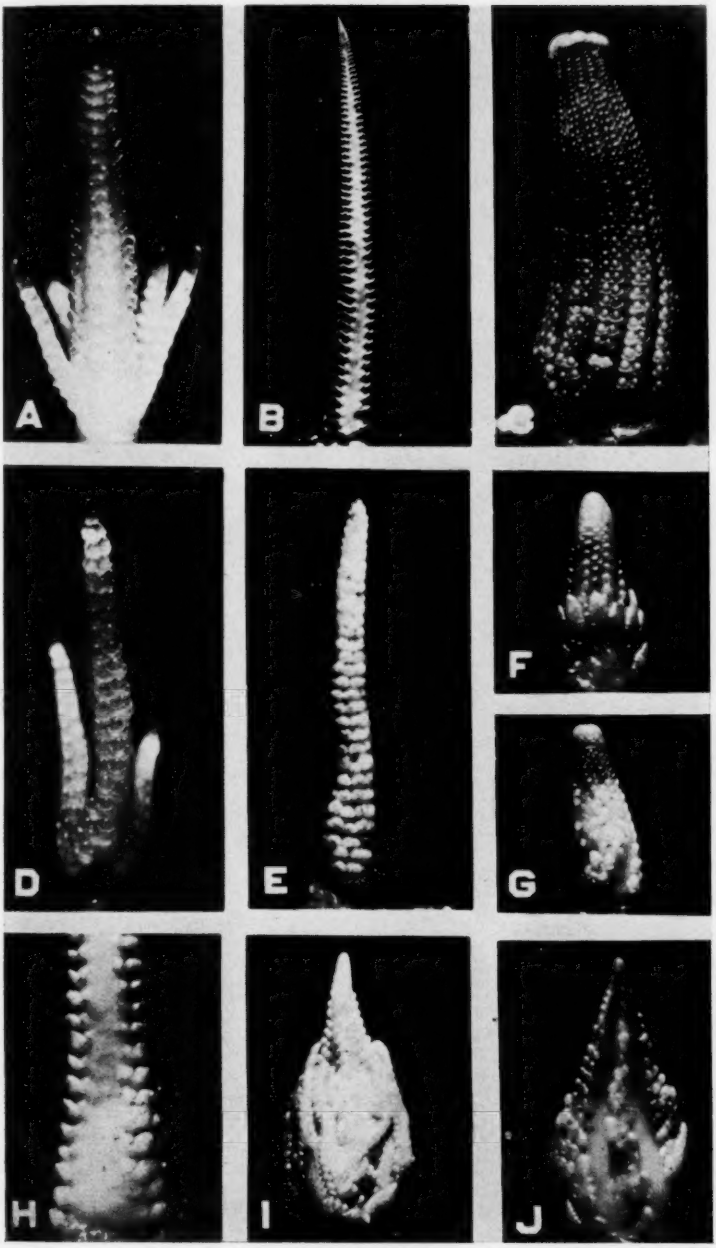
E—Ear of four-rowed corn.

F—Tassel of Japanese Hull-less. The central axis is blunt and thick.

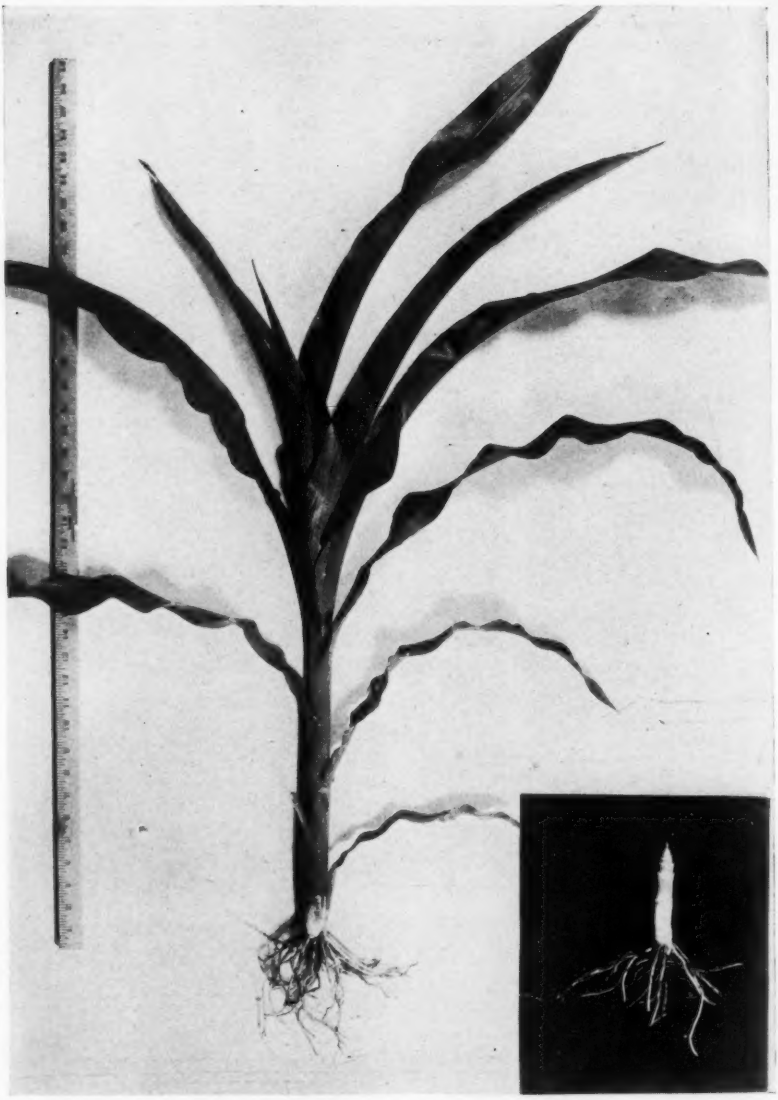
G—Ear of Japanese Hull-less. The characteristics of the ear are similar to those of the central axis of the tassel.

H—Side view of a portion of an ear of four-rowed corn. The spikelets are arranged in two ranks.

I and J—Ears of ramosa or branched-ear corn. Branch elongation is carried well up to the tip of the ear.



BONNETT—EAR AND TASSEL DEVELOPMENT



BONNETT—EAR AND TASSEL DEVELOPMENT

Explanation of Plate

PLATE 31

At the left is a corn plant, and at the right is a plant from which all of the leaves have been removed. The tassel can be seen at the tip of the stem of the stripped plant. Ear shoots are too small to be seen.

A COMPARATIVE DEVELOPMENTAL STUDY OF A DWARF MUTANT IN MAIZE, AND ITS BEARING ON THE INTERPRETATION OF TASSEL AND EAR STRUCTURE

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The homologies of tassel and ear structure in maize, and the problem of the morphological relationship between the inflorescences of maize and other genera in the Gramineae, have provided a fascinating study for many workers. Mangelsdorf (1945) has lately compiled a critical review of the earlier contributions to these problems, and with the aid of more recent data has endeavored to formulate a hypothesis incorporating the main features of previous theories. It is interesting to note that most workers have considered the maize inflorescence (tassel or ear) as a unit for comparative study which is complete in itself. Anderson (1944) first realized the importance of considering the structure of the inflorescence as a culmination of developmental processes which are common to the plant as a whole. It would seem that a study of the inflorescence apart from the rest of the shoot might neglect a very valuable source of information, and that a better understanding of the general developmental plan in the maize plant might furnish a new line of attack in interpreting the particular morphology of the inflorescence.

Adopting this line of approach, the problem of ear and tassel homologies involves three ontogenetic questions:

(1) Bonnett (1940) showed that the primordia giving rise to lateral branches, and the primordia giving rise to paired spikelets on the main axis of the tassel, are homologous structures. Paired spikelets may therefore be regarded as greatly reduced lateral branches. Is this reduction peculiar to the tassel or is it the culmination of a process initiated during the vegetative phase?

(2) Mangelsdorf (1945) concluded that the ear of maize as exemplified by the female inflorescence of Guarany pod corn is "fundamentally identical with the spikes of certain other species of grasses . . . . and like many of them is probably derived from a panicle as the result of reduction of branches. There is not the slightest evidence of fusion." Without in any way disagreeing with the first part of this statement, it may be pointed out that from the developmental point of view the morphology of the panicle represents the crux of the problem; namely, by what developmental process is the simple alternate (distichous) arrangement of primordia, as seen in the basal vegetative portion of the shoot, transformed into the polystichous arrangement found in the apical reproductive region.

(3) Bonnett's developmental studies have shown that the florets of both male and female inflorescences are potentially hermaphrodite. What factors determine

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whether the anthers shall degenerate leaving a pistillate inflorescence in the ear, or the pistil degenerate leaving functionally male flowers in the tassel?

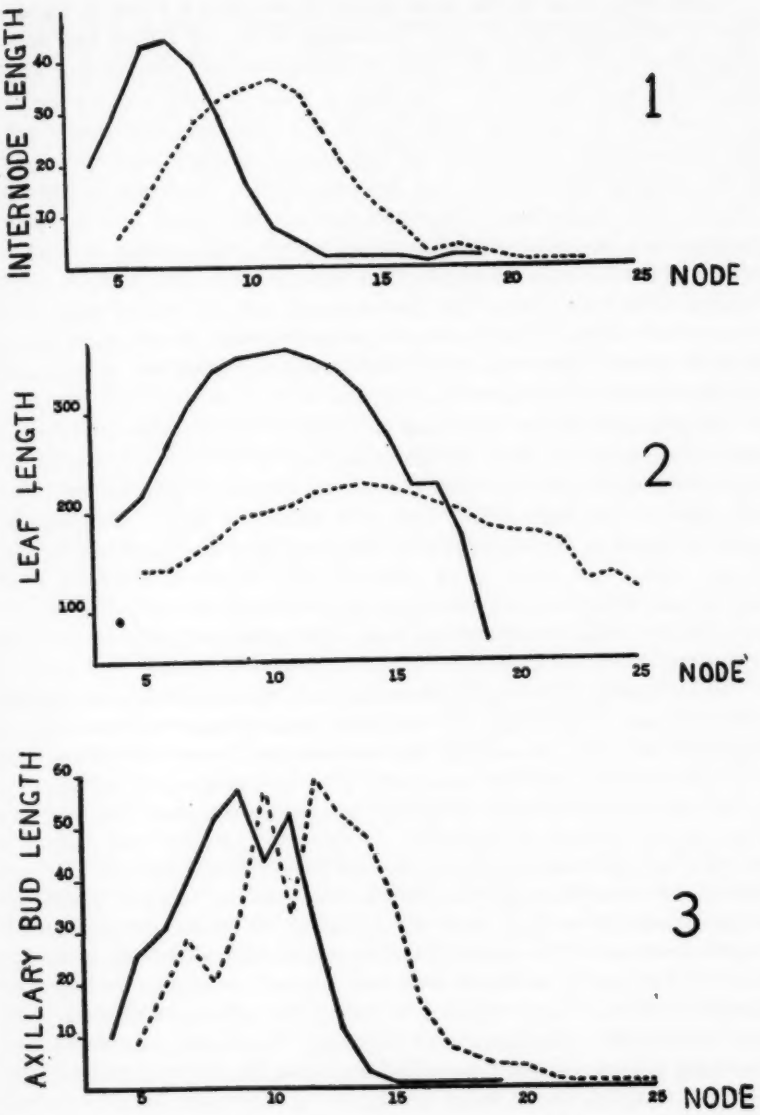
The writer's interest in these problems was first aroused by Dr. Edgar Anderson, who suggested that the disturbances in the normal pattern of development which are found in certain dwarf mutants in maize might be of value in interpreting ear and tassel morphology. A dwarf mutant which occurred as a simple recessive in one of her inbred strains was kindly handed over to the writer for study by Dr. Barbara McClintock. It is the purpose of this paper to report the results of a preliminary comparative study of this mutant and its normal sib, which are believed to have some bearing on the interpretation of tassel and ear morphology.

COMPARISON OF THE DEVELOPMENTAL PATTERN IN NORMAL AND DWARF PLANTS

The dwarf mutant segregated out as a simple recessive from a strain, B 97(1). Spontaneous chromosome breakage had occurred in this same strain but the particular line considered in this paper was cytologically normal. In 1945 two plantings of a line heterozygous for the mutant were carried out; the first in March and the second in June. Mutants and normal sibs were therefore available for developmental comparison from the two plantings.

First planting.—It was possible to distinguish mutant plants in the 6–8 leaf stage, as the leaves were shorter and narrower than in normal plants and tended to project at right angles from the main axis. At a later stage the shorter internodes, with the edges of each leaf sheath closely overlapping its neighbor, gave the plant a sort of "cross-gartered" appearance. Tassel emergence occurred at about the same time as in the normal sibs, but owing to the crowded internodes in the mutant, the tassel was never fully exserted above the topmost leaf sheath. Ear shoots were produced later (i.e. at higher nodes) than in the normal sibs, so that the general picture when the silks emerged was a dwarf plant, about half the normal height, with compressed internodes and the upper leaves, ears, and tassel all bunched together at the apex. The clubbed appearance was accentuated by the fact that in no case did the mutant plants tiller, in contrast to the normal sibs which produced 1–3 tillers.

At tassel emergence three normal and three mutant plants were dissected into their component leaves, axillary shoots, and main stem. Measurements of leaf lengths, internode lengths, and lengths of axillary buds were carried out. The first distinguishable node at the base of the stem was considered Node 1, and on this basis average measurements for corresponding parts were determined for normal and mutant plants. A general picture of the course of development during the vegetative phase was obtained by plotting these average values against their corresponding node numbers as shown in figs. 1, 2 and 3. Although the measurements represent averages of only three plants, the curves obtained are relatively smooth and are deemed adequate for illustrative purposes.



Figs. 1–3. Comparative dimensions of normal and mutant plants at time of tassel emergence as shown by internode lengths (fig. 1), leaf lengths (fig. 2), and lengths of axillary buds (fig. 3), associated with successive nodes of the main axis. Normal shown by solid, mutant by broken line.

Examination of the figures shows that in all cases there is a peak in vegetative vigor as measured by size of parts. Internodes, leaves, and axillary buds become progressively larger during the course of development and then decrease in size towards the apex of the shoot. The stage at which the peak occurs is probably associated with the beginning of the reproductive phase, since dissection of young normal plants when 10–12 leaves had been exserted usually showed tassels in the earliest stages of differentiation (c.f. Bonnett, 1940). The largest axillary buds (fig. 3) mark the position of the future ears. In the case of both normal and mutant plants the peak is reached first in internode length, second in length of axillary bud, and third in leaf length. This sequence agrees with Sharman's (1942) detailed studies which showed that during development a "wave of maturation" commences at the tip of each lamina and passes downward through the sheath and internode below. Maximum length should therefore be attained earliest in the lamina and latest in the internode.

Comparison of the data for normal and mutant plants shows that for the three series of measurements shown in the figures, the vegetative peak is reached at a later node in the mutant. At tassel exsertion the mutant has produced more nodes and therefore, also, more axillary buds with subtending leaves. Internodes and leaves are shorter in the mutant than in the normal plant at a corresponding stage, though axillary buds appear to be similar in size. In general, the effect of the mutant gene appears to be a disturbance of the normal pattern of development such that the nodes are differentiated more rapidly, but the growth of associated structures (leaves, axillary buds, internodes) is markedly reduced.

Second planting.—No essential differences from the first planting were noticed during the early stages of growth. As before, mutant plants could easily be distinguished from their normal sibs. At tassel exsertion, however, a striking effect of the late planting conditions was manifested by both mutant and normal plants. In the earlier planted material neither mutants nor normal plants had shown any abnormality in tassel or ear characters. In the mutant, the ears were crowded in the upper leaf axils around the tassel but they were structurally normal. By contrast, at the second planting, while the main axis tassels of "normal" plants were always structurally normal, nearly all the tillers had tassels partially modified towards femaleness. The degree of modification varied considerably; in extreme cases the whole central axis of the tassel was converted into an ear, the laterals remaining staminate, while in milder cases only a few spikelets at the base of the tassel were pistillate. Such partial sex reversal in tillers is not uncommon in certain strains of corn, and is the general rule in others, but the strain under investigation had shown no trace of such a tendency at the earlier planting. It is probable that the environmental factors responsible were either the short day length or cold night temperatures occasioned by the late planting, since both these factors are known to modify the phenotype considerably (Purvis and Gregory, 1937; Went, 1944).

In the case of mutant plants no tillers were produced and dwarfing was more pronounced than at the earlier planting. Dissection showed that the uppermost nodes were extremely crowded, and always telescoped into each other to some extent (pl. 32A). As a result of this crowding the zone of nodes bearing no axillary buds, which normally exists between the uppermost ear-bearing node and the base of the tassel, was almost completely eliminated. Instead, there existed a continuous series of lateral branches, the lowermost members of which were normal ears borne in the leaf axils, and the uppermost members were paired spikelets arising directly on the main axis with no subtending leaf. Between these extremes a continuous graded series could be arranged which is illustrated in plate 32B. The top row from left to right in the plate represents branches borne in the axils of the upper leaves at progressively younger (higher) nodes. The first member of the series does not differ essentially from the normal ears borne at lower nodes, although the ear is very small and the sheathing husks reduced to two. The rest of the series shows a progressive conversion of the ear into a structure indistinguishable from a lateral tassel branch except for a single reduced "husk" at the base. The lower row in the plate shows a continuation of the series, representing lateral branches which occurred above the topmost leaf, i.e. they had no subtending leaf. This continuation of the series shows a graduation from a lateral tassel branch to a paired spikelet borne on the main axis.

Since the effect of the mutant gene at the earlier planting was to crowd the ear-bearing nodes towards the tassel (fig. 3) as compared with the normal plant, its effect at the later planting may be regarded as a more extreme expression of the same process. Here the crowding has been so great that the normally clear-cut sequence—ear-bearing nodes, nodes with no axillary buds, lateral tassel branches—has been condensed so that an intergrading series from ear to lateral tassel branch is the result.

DISCUSSION

The homology of lateral primordia in cereals.—The work of Purvis and Gregory (1937) on the vernalization of winter rye showed that double primordial ridges, occurring at the lower nodes of the main axis in the early stages of development, and the spikelet initials, found at the apex of the shoot, are homologous structures. Towards the base of the shoot the lower ridge in each double primordium develops into a foliage leaf, while at the upper nodes the lower ridge fails to develop and the upper ridge forms a pair of spikelets. The node at which the switch from leaf-forming to spikelet-forming primordium takes place could be varied experimentally by low temperature pre-treatment and also by variation in day length. That this developmental plan is common to all cereals seems likely. Bonnett's developmental studies *(loc. cit.)* of the inflorescences of wheat, barley and oats, showed that at the beginning of differentiation each spikelet is subtended by a lower ridge, which he interpreted as being homologous with the foliage leaves

borne at the lower nodes. In maize he noted that only the female inflorescence showed these subtending ridges. Certain species of barley regularly have their lower spikelets enclosed by large leaf-like structures, clearly homologous with the leaves borne at lower nodes. Occasionally, too, in oats an aberrant plant occurs in which a structure indistinguishable from a lateral panicle branch is borne in the axil of the topmost leaf sheath. Sharman (1942) concluded that the subtending leaf and the axillary bud occurring at each node of the shoot are botanically unrelated structures, the former being anatomically associated with the internode below, and the latter with the internode above. However, whether it is more correct to think of double primordia, or two distinct initials which are always borne in juxtaposition, does not affect the main issue—the homology of tassel branches and axillary buds (ear-shoots). The mutant described in this paper, which exhibits a continuous range of expression from axillary ear shoot to lateral tassel branch, provides developmental evidence of the correctness of the anatomical theory.

Since tassel branches and axillary buds (ear shoots) are homologous, they must represent different stages in a developmental series and it might be expected that the developmental processes which have operated in forming the tassel would leave traces in axillary buds, i.e. in ear shoots and tillers. This expectation is supported by Anderson's discovery (1944) that degree of condensation of the lateral tassel branches is strongly correlated with the number of rows in the ear. It would seem that where an unbroken series of primordia can be induced to develop, as in the mutant described here, it should be possible to distinguish acropetal gradients in the processes affecting the development of the inflorescence. These may be considered in relation to the three questions suggested in the introduction of this paper.

Reduction of lateral branches.—Reference to pl. 32B shows that in passing from lower to upper nodes, i.e. from ear-bearing nodes to nodes bearing paired male spikelets, there is a gradual decrease in the number of parts borne by the axillary branches. This begins as a reduction in the number and size of the husks enclosing the lateral branch (see top row) and continues as a reduction in the number of spikelets (see bottom row). In the normal maize plant this progressive series is broken, because the intermediate stages are suppressed (there is a zone of nodes between the topmost ear-bearing node and the node bearing the lowermost tassel branch, which carries no axillary buds). The disturbance in normal development exhibited by the dwarf mutant eliminates the sterile zone and in doing so clearly demonstrates that reduction in spikelet number in passing from base to tip of the main axis of the tassel is but a continuation of a process initiated earlier in the vegetative parts of the plant.

Condensation of nodes.—Condensed nodes were frequently found in the main axis of mutant plants, an example of which is illustrated in pl. 32A. In this illustration the number of leaves borne at each "node" or condensed group of nodes is

indicated by the white figures. The lowest "node" shown in the illustration carried two leaves and it can be seen that the "node" really consists of two adjacent nodes with a very short internode between. The next "node" bore six leaves, which suggested that it consisted of a complex of at least six nodes, though only two nodes joined by a spiral ridge are visible externally. The four higher "nodes" bore no leaves and appear to be simple, but the fact that they bore three, five, and five lateral branches respectively, throws doubt on their apparently simple structure and suggests rather that each "node" is in reality a complex of several nodes.

Other evidence of condensation is illustrated in pl. 33. The leftmost picture (a) shows a portion of a tiller of a normal plant which bore a tassel partly modified towards femaleness (tassel-ear). Examination of many such tassel-ears showed evidence of node condensation. Next in order from left to right (b) in pl. 33 is a portion of an axillary branch which developed at a node below the usual ear-bearing region in a normal plant. This branch was induced to develop by extirpating the main axis tassel at an early stage of development. Although a normal ear was borne by this branch, the shank is greatly elongated and structurally similar to a tassel-bearing tiller, but shows condensation of nodes. The two rightmost illustrations (c) and (d) from normal plants show ears borne on long shanks which again show node condensation. In the case of all four branches illustrated in the plate, the nodes below the condensed region bore only one leaf per node, but above the condensed region, more leaves than visible nodes were always present. *This condition would seem to be true for normal ear-bearing branches in general, since careful examination shows that the number of husks enclosing the ear is always greater than the number of distinct ridges on which they are borne.*

It seems to the writer that the association of the ear structure with a region of condensed shank nodes immediately below it may be of developmental significance. Examination of many condensed regions similar to those illustrated in pl. 33 suggests that condensation begins with a twisting of the axis. If the twisting is severe, the node becomes tilted to one side and fused with the node immediately below. In other words, the series of separate ridges becomes converted into a continuous helical ridge. Further twisting results in a suppression of the internode between the gyres and a consequent fusion of neighboring gyres. When neighboring gyres are fused a multiplication of axillary structures (leaves and axillary buds) results. The stages leading to this multiplication can only be recognized in suitable material like that illustrated in pl. 33, but it may be suggested that an acceleration of the same process underlies the multiplication of spikelets in both ear and main axis of the tassel. If this interpretation is correct, the "nodes" of the male and female inflorescences which exhibit a polystichous arrangement of spikelets represent complexes of nodes, each sub-unit of which bears two spikelets. The condensation initiated in the shank would be continued and intensified in the ear itself. The normal tassel, since no leaves subtend the lateral branches, provides no

clue as to its complex nature, but the same underlying structure seems evident from the condensation exhibited by the abnormal mutant tassel illustrated in pl. 32A. Furthermore, this interpretation appears to be the simplest way of explaining the correlation between degree of tassel condensation and ear row number which has been demonstrated by Anderson (1944).

It might be argued that the chance fusion of nodes with accompanying multiplication of parts could only produce an irregular arrangement of spikelets in the inflorescence, whereas the row number found in the ear is a very regular and constant feature. This, however, would ignore the obvious, though little understood, laws of organized development which underlie phyllotaxy. The mechanical precision with which repeated structures are arranged in relation to one another has been stressed by Thompson (1942). He has shown that diverse problems of phyllotaxy may be interpreted, though not explained, in terms of rather simple mathematical constants. Thus the position of an axillary bud, pair of spikelets or leaf, appears to pre-determine or (in the mathematical sense) generate the position of the corresponding structure at the succeeding node. In a perfect alternate distichous arrangement, one structure generates the position of the next at an angle of 180° in respect to the main axis. If the angle is a little more or a little less than 180° a helical twist is superimposed on the distichous arrangement, as can often be seen in the arrangement of leaves on a young maize plant. Now, if two nodes become fused, it would appear that each pair of spikelets would act as independent generators in the production of spikelet pairs at the succeeding node, and this process might be expected to continue in an orderly fashion without further fusion of nodes. In short, a 16-row ear does not require a repeated fusion of nodes in groups of eight, but merely that eight nodes shall be condensed *once*, and that the eight spikelet pairs shall each generate a spikelet pair at successive nodes. Since an apparent fusion of six nodes can be seen in the abnormal tassel shown in pl. 32A, fusion of this order would not appear to make undue demands on the anatomical structure of the axis. It may be noted that the mechanisms suggested would be applicable to panicles in general, and not confined to the maize inflorescence.

If condensation of nodes is the explanation of the change from a distichous to a polystichous condition, there would appear to be a gradient of increasing condensation from the base to the apex of the main axis, and from the base to the apex of all axillary branches, i.e. in the tassel from the lower distichous lateral branches to the upper polystichous central axis; in the ear shoot from the lower nodes in the shank bearing distichous sheathing husks to the upper spikelet bearing nodes which are all polystichous. Normally, condensation is synchronized rather closely with the switch from vegetative primordium to spikelet initial, but when the synchronization is disturbed, either by environmental effects or by mutation which modifies the normal growth processes, as in the mutant described here, the mechanism of condensation can be observed in the vegetative phase of development.

The determination of maleness and femaleness.—The material considered in this paper sheds little light on the mechanism which determines whether male or female spikelets shall be produced. Within the restricted limits of the material examined, however, the following generalizations appear to be valid:

(1) An axillary branch bearing an inflorescence which exhibits a greater or less degree of femaleness is usually associated with obvious condensation in its lower, leaf-bearing nodes.

(2) In inflorescences of mixed sex, it is the more condensed nodes which tend to bear female spikelets. Thus it is usual for the central condensed axis of a tassel-ear to bear female spikelets; the lateral, less condensed tassel branches are preponderantly male.

(3) Tillers (i.e. axillary branches which develop independent root systems) bear tassels or tassel-ears. Axillary branches, when induced to develop by tassel extirpation at nodes *below* the normal ear-bearing nodes and *above* the tillers, usually bear ear-shoots.

(4) The inflorescence borne at the apex of the main axis and the inflorescence borne at the apex of a tiller are labile in respect to sex; the switch mechanism being affected by day length and/or thermoperiodicity.

SUMMARY

(1) A comparative developmental analysis of a recessive dwarf mutant with its normal sib in maize suggests that the dwarfing gene: (a) increases the production of nodes and associated axillary structures; (b) reduces the lengths of the internodes, leaves and leaf sheaths; (c) delays the production of axillary ears so that the sterile zone, normally existing between the uppermost ear-bearing nodes and the lowest tassel branches, tends to be eliminated.

(2) Under suitable conditions the axillary branches in the dwarf mutant exhibit a graded series, ranging from normal ear to paired male spikelets.

(3) Within this graded series the following tendencies are evident:
  (a) Progressive reduction in number and size of the lateral organs borne by the axillary branches in passing from base to apex of the main axis.
  (b) Progressive condensation of nodes from base to apex both in the tassel and in ear-bearing axillary branch (shank).
  (c) Association between degree of condensation and femaleness.

(4) The observed tendencies are used to suggest a probable interpretation of the morphology of tassel and ear in the normal maize plant.

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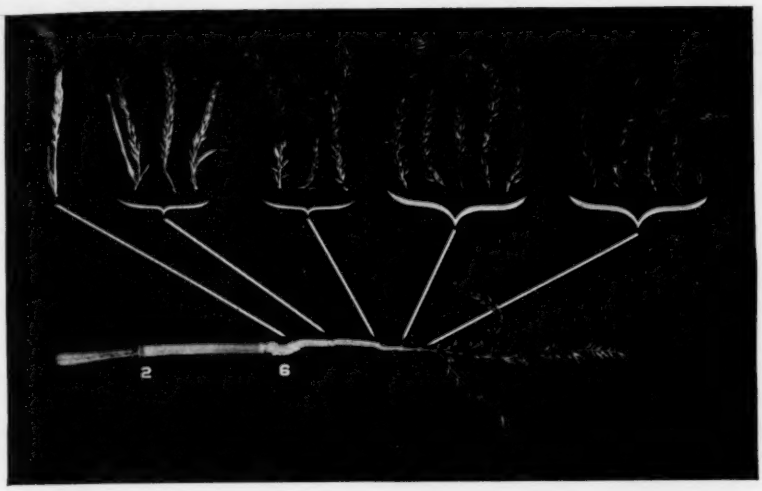
Explanation of Plate

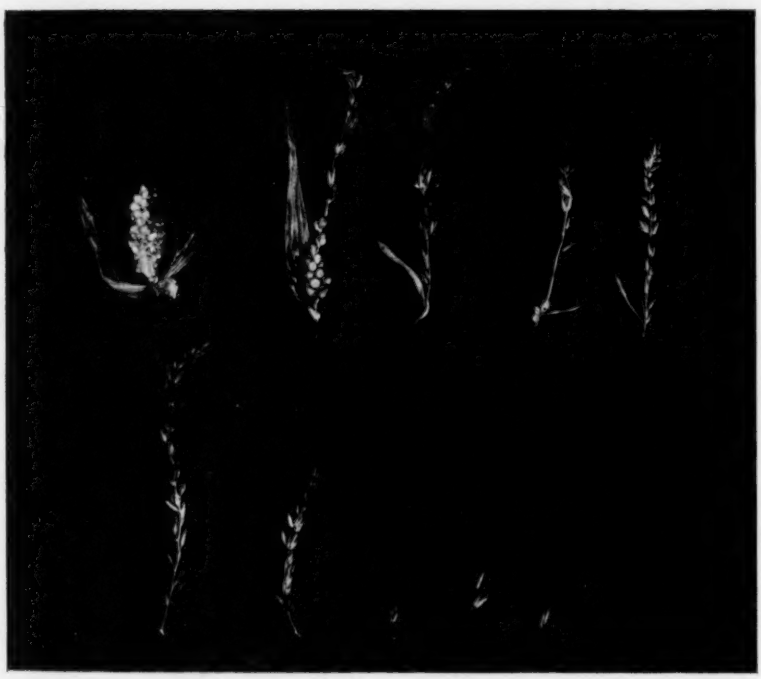
PLATE 32

Fig. A. A dissected tassel and uppermost nodes of the main axis in a late-planted mutant. Figures indicate the number of leaves removed from each node; the position of the lateral branches is indicated by lines.

Fig. B. A range of lateral branches occurring in late-planted mutants, in a region corresponding to the sterile zone of the main axis in a normal plant. Upper row—lateral branches borne in the axils of foliage leaves; lower row—lateral tassel branches arising at nodes with no subtending leaves.

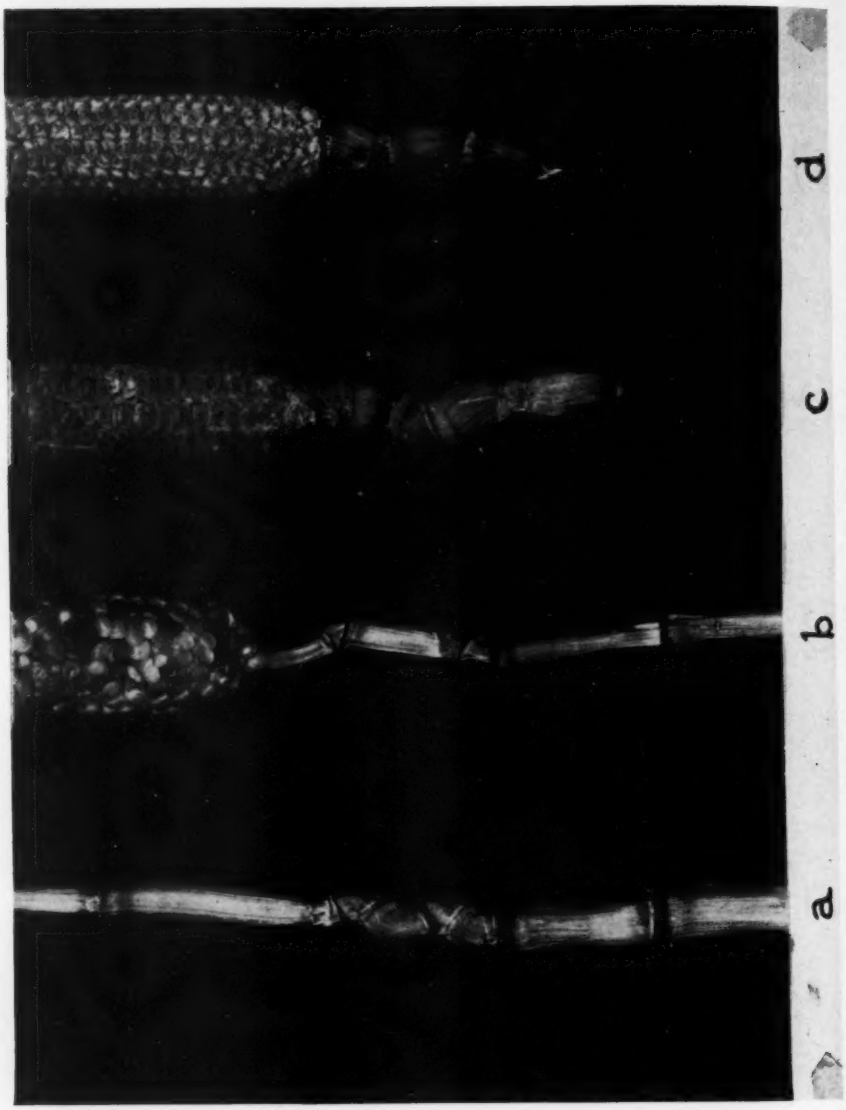


A



B

STEPHENS—TASSEL AND EAR OF DWARF MUTANT



STEPHENS—TASSEL AND EAR OF DWARF MUTANT

Explanation of Plate

PLATE 33

Evidence of node condensation in "normal" plants. From left to right (a) main axis of a tassel-ear, (b) female axillary branch induced to develop by tassel extirpation below usual ear-bearing nodes, (c) and (d) axillary branches bearing normal ears on abnormally long shanks. In all cases at nodes below the condensed region leaves were borne singly, while nodes above the condensed region bore two or more leaves each.

STUDIES ON THE STRUCTURE OF THE MAIZE PLANT

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There is a basic pattern for most grasses and this pattern is repeated throughout each plant, in reproductive as well as vegetative parts. The main axis of the maize plant bears leaves and buds on opposite sides of successive nodes. This pattern extends to the branches, the tassel, and to the ear. In the maize tassel and ear the parts and even their arrangement may be modified, but the basic arrangement is still that of the stem of any grass. This can be seen easily in the lateral branches of the tassel and in ears with only four rows of grain.

All parts of the maize plant are made up of similar units. The name "phytomer" has been applied to these (see Esau, 1943, for a discussion of this as applied to the stem). A phytomer consists of an axillary bud at its lower end, a section of the stem (the internode), and is terminated by a leaf. It corresponds to Collins' (1919) *alicole*, although his original definition included only the spikelet or pair of spikelets and not the associated portion of cob or stem.

Because the maize pattern is repeated throughout the plant we can expect almost any change in one part to be repeated in homologous parts. For example, when hairs on the leaf sheath are large and numerous, there will be large and numerous hairs on the glumes of tassel and ear. Because of this repetition of plant pattern, some organs which are not strictly homologues will reflect changes in other parts. Thus, in one race of Bolivian maize, when the tassel branches and the rows of spikelets on the central spike are nearly doubled in number, the number of rows of grains on the ear and vascular strands in the stem are correspondingly increased.

The extent of variation in the grasses is greatest in the flowering parts and least in the vegetative areas of the plant. Thus the leaves are still arranged dichotomously in the Bolivian maize even though the number of tassel branches and rows of grains has been doubled.

MATERIALS

Maize.—

We studied most of the known varieties of maize in our plantings in Brazil, Bolivia, Cuba, and the United States. Some others we were able to study in the field or in dried specimens of ears. Plant-breeders and geneticists furnished material of especially interesting mutants. Two collections of this material were of great interest. One was the Central American and Mexican maize assembled by Dr. Paul C. Mangelsdorf and from which many chromosome knob positions had been determined by Dr. James Cameron. The other was a collection of inbred lines for which Dr. William L. Brown had mapped chromosome knob positions.

Teosinte.—

Some teosinte was collected in Guatemala but most of the studies were based on material grown from seed in Bolivia. For convenience we use the common name, teosinte, instead of the combination *Zea mexicana* (Shrad.) Reeves & Mangelsdorf.

Tripsacum.—

Most of the studies were made on *Tripsacum australe* Cutler & Anderson, not only because this was the one on hand when the work was under way in Brazil but because it has been reported to lack terminal knobs on the chromosomes (Graner & Addison, 1944), and is the most southern of the 18 (n)-chromosome *Tripsacum* species.

Manisuris cylindrica (Michx.) Kuntze.—

Material of this species was collected in Texas and Florida. A series of related varieties was studied in herbarium material from southeastern United States.

METHODS

Most of the studies were made on dried ears and tassels. The cobs and glumes of many varieties, especially some from North and Central America, were hard to dissect so young green ears grown in Brazil, Bolivia, Cuba, and the United States were used for these varieties. Young ears have nearly all the characters of a mature ear except color.

In cases where paraffin sections were desired, ears collected the day the silk appeared were fixed in Carnoy's fixative. At this stage most of the structures are fairly well formed, although their relative sizes are not the same as those in the mature ear. After being embedded in paraffin these ears could be cut easily and safranin- and haematoxylin-stained sections studied and compared.

Many cross- and longitudinal-sections of the stem and ears were cut free-hand and photographed by floating them onto a glass plate in the negative holder of an enlarger. The projections of these sections, made on standard enlarging paper, were studied, compared, and measured more accurately and rapidly than would be possible with the sections themselves.

When the retting methods described by Evans (1928), Sharman (1942), Reeves (1946), and Laubengayer (1946) are applied carefully, good preparations with a clearly visible network of vascular strands are obtained. We immersed some bundles in a vial of stain as directed by Evans (1928), but, since we wanted to follow more strands and had only a limited number of plants, it was more convenient to inject the stain with glass tubes which were drawn out to hypodermic needle-like points. With these we could inject several colors and trace their separate courses in the same plant. By filling the tubes one-quarter full of tap water while they were being inserted, staining of the outer rows of bundles

was avoided. Stain was added after the tube was fastened to the stem, tassel, or ear with Scotch tape. Aqueous solutions of eosin, methyl blue, and Bismarck brown were used. The tubes usually were left in place for two days although stain was carried through several nodes in a few hours.

ARRANGEMENT OF THE PHYTOMERS

If one considers the maize plant to be made of units which are moved into place like bricks in a house, then it is necessary to consider the plant as based on a spiral arrangement with each unit rotated 180 degrees. This makes the polystichous structure of the ear and the central spike of the tassel dependent only upon a change in the pattern of phyllotaxy (Weatherwax, 1935), a change which can be seen in other plants (Brieger, 1945). There have been attempts to trace this pattern in the ear and tassel. The method which shows greatest promise has been used by Mangelsdorf (1945) and takes advantage of the fact that in the distichous lateral branches of the maize tassel, and in the staminate inflorescences of teosinte and *Tripsacum*, the two rows of paired spikelets are arranged so that the pedicellate spikelet of one pair is adjacent to the similar spikelet of the other. Thus as one goes around a staminate branch of maize, teosinte, or *Tripsacum*, the spikelets are sessile, pedicellate, pedicellate, sessile. The main difficulty in applying this method is that the vertical distance between paired spikelets of the tassel is not always the same and it is necessary to measure carefully. In the ear, on the other hand, this distance is quite constant, and notations of the sessile and pedicellate spikelets can be made on squared paper. With many ears it is difficult to distinguish between pedicellate and sessile spikelets and on some ears practically impossible (Cutler, 1946). Where we have been able to apply this method to the ears, our results agree substantially with those of Mangelsdorf. There is a strong tendency to a longitudinal arrangement, a tendency made conspicuous by the vertical course of conductive tissue.

The major vascular strands run longitudinally, and although there are some connections at the nodes these are so weak that very little stain is carried to other rows of phytomers. The weakness of these connections may be seen in some maize ears with a large cob. Most of these will split longitudinally between rows of paired spikelets but resist breaking between the paired spikelets of a row, and to a lesser extent, across the rows of paired spikelets.

As an aid to the study of the relationship of the parts of the plant, we found it convenient to study the course of the vascular system. The plant may be considered to be made up of leaves, the stem to be composed of leaf traces. In the upper parts of the tassel, the number of vascular strands in the main axis is very small, and the number increases as we descend the stem and the traces of more leaves enter. Plants with many tassel branches, many nodes, and many rows on the ear usually have many vascular bundles. The number of vascular bundles in an ear appears to be larger in those ears with more grains in a longitudinal row.

An apparent contradiction to this is found in the position of ears on a single plant. Usually the highest ear has the largest number of rows of grains, and those ears borne lower on the stem, although there are more vascular bundles in the stem at the node from which these ears originate, have smaller numbers of rows of grains. In lines studied by Burdick (1947), the uppermost ears usually had eight rows of grains while the lower ears usually had four rows. Burdick attributes this to the differentiation and development of the lower ears under less favorable physiological conditions. In our observations on a large number of varieties with a wider range of row numbers, we have found Burdick's observations to be valid. Exceptions are found when a large number of ears are borne on one plant as happened on one of our crosses of Bolivian highland maize with Golden Bantam. The ear borne at the sixth node had twelve rows of grain; those at the fifth and seventh nodes had ten; at the fourth, ten; at the third and eighth nodes, eight rows. An undeveloped ear at the second node had eight rows. With the exception of plants with eight-rowed ears our notes on South American maize plantings show that the number of rows of grain on two ears from the same plant is rarely ever the same. Our notes also show that in most varieties, and again we except those which bear ears with eight rows of grains, the number of rows on the ears is greater on plants with a higher number of nodes and a higher number of vascular bundles.

There are two groups of vascular strands, the peripheral and the central or medullary. The strands pursue a nearly vertical course and these systems tend to remain distinct. When the traces from a leaf or homologous structure enter the main axis, most larger and more median bundles go almost immediately to the central region while the smaller bundles remain in the periphery and after a few nodes unite with some of the other peripheral bundles or progress to the center. The two systems are present in stem, tassel, and ear of maize, and in homologous parts of teosinte, *Tripsacum*, and *Manisuris*. The vascular system of the maize stem has been studied by Hershey and Martin (1930), Esau (1943), and Kumazawa (1940); that of the tassel by Kumazawa (1939, 1940a), and that of the ear by Reeves (1945, 1946), and by Laubengayer (1946). While there have been some studies on the relation of the stem structure to stiffness of stalk (Magee, 1948), none of the investigators has worked with a wide variety of material. There is an opportunity here for investigations of considerable practical value especially now that mechanical corn pickers are used and lodged corn stalks are more of a nuisance.

AXIS, STEM, RACHIS, COB

The axis is usually somewhat cylindrical in the stem and other distichous parts, but in a polystichous axis, like that of a many-rowed ear, the axis of each phytomer is a pie-shaped segment. Usually there is a hollow above the bud or branch. In the stem and tassel this is a longitudinal groove and in the ear a pit

or alveole. The alveole is very pronounced in teosinte, *Tripsacum*, and *Manisuris*, and its margins may partially enclose the spikelet. In some South American races of maize like "Coroico" (Cutler, 1946) and some varieties from the highlands of Peru and Bolivia and parts of Chile and Ecuador these margins or rachis flaps are inconspicuous. In other varieties, especially some of Mexico and southwestern United States, they are prominent.

For a long time we thought that prominent rachis flaps were always associated with *Tripsacum*-contaminated maize and with a high number of knobs on the chromosomes. Using chromosome knob positions determined by Dr. James Cameron for a large number of Guatemalan and South American samples of maize, and positions determined by Dr. William L. Brown for a selection of common commercial inbreds, we tried to find some correlation between the presence or absence of certain knobs and variations in the structure of the maize spikelets, both male and female. In some of the Guatemalan material there appeared to be a good correlation between prominent rachis flaps and the presence of a knob on the long arm of chromosome 3. Examination of more material showed us that not only was this incorrect, but that rachis flaps are not always correlated with high knob numbers. Some of the North American inbreds with only one chromosome knob have more prominent rachis flaps than others with seven or eight knobs.

The rachis flap resembles the auricle of the leaf in shape and this resemblance is heightened by the presence below it of the pulvinous notch, a small notch often formed at the margins of a leaf, bract, or glume, at the point of its union with the node. Like an auricle notch, it usually bears numerous hairs.

The sulci, or grooves between rows of alicoles or phytomers of the maize ear, are often deeply cut into the cob. We have found no definite geographical distribution of sulci, but they are most prominent in many-rowed ears from the Andes, Mexico, and our Southwest. In some races, as Coroico, and Altiplano from the Bolivian highlands, sulci are rarely ever present.

The vascular strands supplying the paired spikelets of the maize ear may separate nearly at once after branching out from the longitudinal vascular system but often may remain together for several millimeters. The latter is the case in some South American maize and in these varieties the paired spikelets are usually raised above the alveole. In marked contrast to this are spikelets attached so closely to the cob that they are turned toward the tip of the ear and do not lie perpendicular to the longitudinal axis of the cob.

The rachilla on which the spikelets are borne is surrounded in part by the glume. About the base of the rachilla of each spikelet of the ear is a small callus. One of the pair of spikelets is usually borne lower on the glume than the other and is surrounded by a small ring of unicellular hairs. This lower spikelet appears to correspond to the sessile one of the tassel. The rachilla of the maize spikelets is variable in thickness and in the length of its internodes. In some *Tripsacum*

and in *Manisuris* the rachilla is quite slender and the glumes, lemmas, paleas, and other parts are well separated. In teosinte and other species of *Tripsacum*, notably *T. dactyloides*, the rachilla is compacted and the parts close together. The grains of corn ears which have glumes raised above the ear and have longer and/or more slender rachillas can be pushed into the ear. The sessile ones with a compacted and short rachilla are firm. In most Guatemalan maize Andean varieties (Mangelsdorf & Cameron, 1942) could be distinguished from tripsacoid varieties by the ease with which the first could be pushed in. Ease of shattering is related not alone to the longer rachilla but to the weaker attachment of the grain to the rachilla. In segregates from crosses of Golden Bantam and Country Gentleman sweet corn many of the grains fell readily from the ear even though they were borne on compacted rachillas. This is a desirable characteristic in corn to be eaten on the cob, for the grains can be removed without the annoyance of particles of glumes and pericarp catching between the teeth. After the grain has been eaten the cob is clean and neat.

THE NUMBER OF SPIKELETS

Many of the Rottboelliae, the tribe of the Andropogoneae to which *Zea* and *Tripsacum* should belong and to which *Manisuris* does, have only one spikelet in each phytomer. In this spikelet are usually two flowers. The upper one is usually perfect and bears both pistil and stamens; the lower one is usually staminate and does not produce seeds. In cases where two spikelets are produced, one is often non-functional or staminate, while the other bears stamens and pistils. In the tassels of maize which bear seed, the sessile spikelets usually bear the seeds while the pedicellate ones remain only staminate. In teosinte and *Tripsacum* the staminate portions of the inflorescence have a pair of spikelets in each alveole, but the pistillate portion usually has only one which is functional, although a second one may occasionally develop into a functional staminate spikelet or even into a functional pistillate spikelet. Occasional clones of *Tripsacum australe* have numerous pistillate alveoles which bear pairs of spikelets. A complete series of the possible combinations in a pair of spikelets can be found in *Tripsacum*, teosinte, *Manisuris*, and maize. They are common in segregates from teosinte-maize crosses. Both spikelets may be staminate or both pistillate. When one is pistillate the other can be a pedicelled or non-functional staminate spikelet or a pedicellate and non-functional pistillate spikelet.

In maize there is nearly always a pair of functional pistillate spikelets. An exception to this was discovered by Langham (1940) in an inbred line of maize while he was making a study of single *vs.* paired pistillate spikelets in teosinte and teosinte-maize crosses. Langham concluded that the single pistillate spikelet of teosinte is governed by a single gene recessive to paired spikelets. Although he makes no mention of the tassels of his plants with single spikelets in the ear, it is probable that the tassels were not influenced by the gene he found, for Langham

was studying other tassel characters and would most likely have noticed any differences. Besides, if it is the same gene as that in teosinte, it is unlikely to have any effect on the tassel because the tassel of teosinte has paired spikelets even though these are single on the pistillate inflorescence.

Hepperly (1948) discovered an ear with single spikelets in an inbred line of corn belt dent, and has been studying this character. Hepperly told us that the tassels of his plants were different and those of the plants we have grown from seeds he supplied usually have the pedicellate spikelet of the pair reduced and nonfunctional but still present. There is a series of degrees of reduction of the one spikelet of the tassel, and it would be interesting to transfer Hepperly's single spikelet character to different races of maize and study any modifier complex which might be present.

Maize plants bearing teopod or corn grass genes are extremely variable in habit and in composition of inflorescences. Frequently in corn grass, and occasionally in teopod, many of the pistillate alveoles will have only one spikelet although both flowers of this may function and the spikelet will have two grains.

Illinois R4 is a corn-belt inbred line used in many combinations for the production of hybrid corn seed, but its rows of grains are usually so irregular that it is used only as the pollen parent. On many ears it is difficult to distinguish definite rows. The tassel is also more irregular than most. In R4 only one spikelet bears grains in some of the alveoles, although the other spikelet is present. The distribution of the alveoles with only one grain is occasionally so regular that the ear has an odd number of straight rows of grain over part of the ear. In spite of this we have been unable to distinguish any constant pattern for the distribution of the undeveloped spikelets.

Extra spikelets in an alveole are common in maize and are occasionally found in *Tripsacum* and *Manisuris*. Often the maize tassel will appear to bear several additional spikelets in each alveole which upon close examination may prove to be two nodes close together. This is caused by condensation of an internode (Anderson, 1944) and is distinct from multiplication (Cutler, 1946) by which additional spikelets are formed by branching within one alicole. Multiplication of spikelets within one alicole is common in the basal rows of many varieties of ears. It produces enlarged butts with irregular rows of grains. The additional spikelets are added in the same plane as the two usual ones and are forced out of line by the surrounding grains.

There are some cases of multiplication of number of spikelets in each alveole of the ear in which the additional spikelets are not borne in the same plane as the two usual spikelets but appear higher up on the ear in the same alicole. The first ears we found were among some of Dr. F. G. Brieger's crosses of pod corn with Chavantes Indian corn. These had four pairs of spikelets in some alveoles, two of them with their first glumes facing the butt and two others with their first glumes towards the tip of the ear (Cutler, 1945). The embryo of the upper grain

in the extra spikelet faced the butt just as would one which would develop in the lower flower of the usual spikelet. The extra spikelets were also found in the tassel.

Another ear with additional reversed spikelets was found in some of Dr. Mangelsdorf's collections. In this case only one spikelet was added to the usual pair but the extra one was reversed just as in Dr. Brieger's material, and the grain, even though produced from the upper flower, had the embryo on the side towards the butt. None of the alicoles on Dr. Mangelsdorf's ear had more than three spikelets and most had the usual two. We do not have a tassel from the same plant and ears grown from this seed did not have the extra spikelets.

Most studies on the structure of the ear substantiate the theory that the ear has arisen by the suppression of branches of an inflorescence. It is not surprising, then, that we occasionally find ears with more than two spikelets in each alicole. There are extremes in which the ear branches freely and looks like a greatly thickened tassel. So numerous and crowded are the branches of the tassel and ear that the plants in some variations do not produce seed. The structure of the inflorescence produced in a plant bearing the gene *ramosa*, a gene which controls one of the extreme branching types, has been described by Kempton (1921).

In most experimental fields one can find examples of flowering branches produced in the ear because they are especially common when the plant is disturbed by the presence of genes like teopod, tunicate and some of the tassel seed genes, which have radical effects, or by unnatural growing conditions, especially a change from the usual length of day to which the plant is adapted.

FLOWERS

Usually a spikelet has two glumes enclosing two flowers. The normal flower of maize, teosinte, *Tripsacum* and *Manisuris* consists of a lemma, a palea, two lodicules, three stamens, and a tricarpellate single-seeded ovary with two stigmas. In some flowers the ovary is undeveloped and in others the stamens do not develop. Functional stamens and ovary occasionally develop in the same flower, and are the rule in the upper flower of the *Manisuris* fertile spikelet.

In the Andropogoneae the upper flower usually is perfect while the lower one does not produce seeds but often bears stamens (fig. 1f). Exceptions to this are common in maize, and in one variety of sweet corn, Country Gentleman (fig. 1c), most spikelets bear two grains. The spikelets of teosinte and *Tripsacum* and *Sorghum* frequently have two grains but we have not seen this in *Manisuris*.

Even though Country Gentleman corn has been grown in many parts of the United States, two-grained spikelets are rare in other varieties of corn in North America. In South America there is no variety of maize which is characterized by two-grained spikelets, but a few spikelets with the lower flower developed are found in occasional ears of almost all varieties of highland maize.

The embryos of grains which develop in the upper flower face the tip of the ear while those which develop in the lower flower face the butt. Not all grains with their embryos on the lower side are produced in the lower flower,

and two exceptions, cases in which the alveoles had more than the usual pair of spikelets, have been mentioned. Another exception is to be found in the tips of ears of northern flint and flour corn. On a few ears we have found occasional twisted spikelets with the grains turned so the embryo faced to one side or even to the butt of the ear.

The lower flower develops later than the upper, and the grain must push into any space left between the earlier-appearing grains. Usually all the grains are so pushed out of line by this that there is no semblance of regular rows. Occasionally, however, the later lower grains are forced out to the side of the upper grains of the paired spikelets and become arranged in a straight row of small grains beside the ones from the upper flower.

The later maturation of the lower flower makes it difficult to see which ears bear the double-grained spikelet character when ears are hand-pollinated early in the season. All the fertilized grains may, if the lower ones have not yet developed silks, be borne in the upper flowers. When the ears are pollinated after the silks of the upper flowers are no longer receptive, grains are produced only in the lower flowers.

In some of Dr. Brieger's Brazilian popcorn we found ears with grains in both flowers but with the lower grain poorly developed and lacking endosperm. In appearance the extra grains resembled the structures described by Weatherwax (1925) as originating in the positions of the flower usually occupied by the stamens. These defective grains in the Brazilian popcorn did not develop in most cases unless the upper grain developed. The absence of embryo and endosperm in most of them suggested that they developed parthenocarpically but needed the stimulation of the normal grain in the same spikelet.

In our plantings of two-grained spikelet varieties in Bolivia, the character appeared to be controlled by a single recessive gene acted upon by several modifiers. In their study on Country Gentleman sweet corn, Huelsen and Gillis (1929) suggested that the two-grained spikelet character was controlled by two recessive genes. Since their classification was based on irregular *vs.* straight rows, it is possible that some ears which had a few of the lower flowers developed escaped notice because only one of the flowers in the spikelet was fertilized. A better way to classify ears for this character is to search for grains with the embryo on the butt side. It is possible that Country Gentleman corn and many of the two-grained spikelet ears from South America may bear an identical single recessive gene controlling development of the lower flowers.

There are several known genes which affect the development of the lower flower. Plants with the tunicate gene often have grains in the lower flower, sometimes even in the tassel. In plants bearing the gene for teopod, for any of the several for tassel seed, for silky, and for the "corn grass" which Dr. Singleton is studying, the lower flower usually develops.

Occasionally the stamens,, as well as the ovary, develop in the upper flower, or even in both upper and lower flowers on the ear. More commonly the tip of the ear bears purely staminate spikelets which are similar to those of the tassel.

Sometimes more than two flowers are found in the spikelets. Weatherwax (1925) has described cases in which several flowers, both pistillate and staminate, were found.

LEAVES, BRACTS, GLUMES, LEMMAS, PALEAS

That the ear of maize, and the central spike of the tassel, too, originated from the suppression of lateral branches is further suggested by the frequent occurrence of small ears in the axils of many of the husks below the main ear. Although husks or bracts are not usually found in the corn ear or tassel, one or two of the lower pairs of spikelets on an ear will occasionally be subtended by them, and the branches of the *ramosa* inflorescence mentioned earlier are often subtended by bracts. Bracts are commonly found subtending the spikelets of two peculiar mutants, teopod and corn grass.

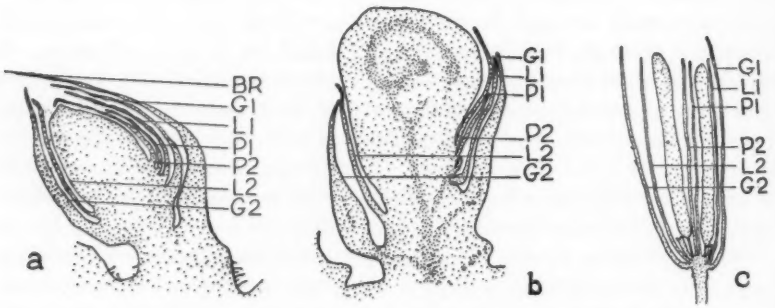

Fig. 1. Median longitudinal sections through a single spikelet of (a) teopod maize ear, (b) normal ear, (c) maize tassel.

Teopod is a dominant mutant gene on chromosome 7 which was described by Lindstrom (1925) and has been studied morphologically by Weatherwax (1929). Plants bearing this gene are extremely variable and many forms resemble teosinte in habit. On most of the plants, each pair of spikelets, in both tassel and ear, is subtended by a bract so large that it completely envelops the spikelets and the ear resembles an ear of pod corn (fig. 1a).

Corn grass is another dominant mutant, discovered by Dr. Bailey Pepper in a field of sweet corn in New Jersey. It is now being studied by Dr. W. R. Singleton and it is with his permission that we cite his first report (1947). In the few plants we grew from seed supplied by Dr. Singleton, the bract subtending the paired spikelets is only occasionally found in the tassel. Many of the lateral in-

florescences have a superficial resemblance to the inflorescence of teosinte with its many spikes each enclosed by a single husk or bract. In corn grass many of the spikelets bear both stamens and pistils.

The position of the bract can be seen in a median longitudinal section of the teopod spikelet (fig. 1a). The bract originates directly above the hump which, with its horizontal vascular system, represents the node. The bract corresponds to the leaf sheath. Occasionally the leaf blade is present, just as in the husks there may be "flags." On the glume we have seen a part equivalent to the blade of the leaf only in a few plants of teosinte and *Tripsacum laxum* in which parts of the staminate spikelet proliferate. The spikelet resembles a bulbil in the inflorescence of an agave plant and a few of them produced small roots.

There are, however, many degrees of development of the part homologous to the ligule, the fringe at the tip of most glumes. An auricle is not present in the glumes unless there is also the part equivalent to the leaf blade. The fringes along

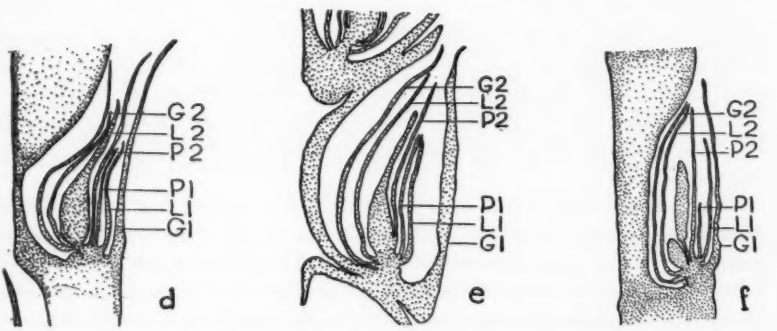

Fig. 1 (cont.). Median longitudinal sections through (d) lower or female portion of *Tripsacum* inflorescence, (e) of teosinte inflorescence, (f) inflorescence of *Manisuris cylindrica*: Br, bract; G1, lower or first glume; G2, upper glume; L1, lemma of first or lower flower; L2, lemma of second or upper flower; P1, palea of first flower; P2, palea of second flower.

the lateral margins of the glumes, lemmas, and paleas represent the margins of the leaf sheath. The keel of the bi-keeled lemma is often, but not always, the line of division between the margin of the sheath and the sheath proper. The sides of the lemma often have a vascular system, and this is lacking in the leaf-sheath margin.

At the base of the lower glume in the pistillate spikelet of the grasses we are considering is a line similar to that between the leaf sheath and the lamina of the usual maize leaf, but homologous to the junction of the leaf sheath with the node. This line is variable in width and color. It is not prominent in the staminate glumes.

We have been unable to find any color pattern of the pistillate glumes and the leaf sheaths which is associated with the glume bar or glume spot on the staminate glume, although this may be masked by other colors. This marking of deep

maroon or purple varies greatly in size, from a small dot to a patch of color covering the lower two-thirds of the maize glume. In most *Tripsacum* it is quite consistently a small spot or triangle.

The maize leaf sheath has prominent ribs marking the vascular strands. Between these one often finds hollows or pits, and there may be many hairs. These surface irregularities and hairs are found in many other grasses and recur in homologous parts of the plant. The most extreme surface irregularities are found on the lower glumes of *Manisuris*. Some of the glumes are so peculiarly sculptured that the forms have been given specific rank (*M. rugosa, M. corrugata, M. tuberculata*, and others), although it is doubtful if all of these should rightfully be considered species. The glumes of maize and *Tripsacum* are often sculptured, and while the sculpturing never reaches the extremes found in *Manisuris* and in *Hackelochloa granularis*, the irregularities are often accentuated by colored markings.

The hairs on the leaf sheaths of maize, teosinte, and *Tripsacum* are usually concentrated along the margins near the auricle. Hairs are usually inconspicuous on the female glumes but they are occasionally present in numbers proportional to those found on the leaf sheath. Some hairs are always present on the staminate glumes, and they may be abundant enough to give the glume a silky appearance. The hairs are nearly always unicellular and vary in shape from short and thick to long and slender.

The hairs which develop in the pulvinous notch, at the point of attachment of the leaf to the stem, or of the glume to the rachis, are often prominent in the maize ear. We have not been able to see material of the "corn cob fur" described by Richey (1946) and cannot be certain of the origin of the hairs in his specimen. From his photographs they appear to have a regular distribution and probably are an extreme development of the hairs on the margins of the rachis flaps, in the pulvinous notches, and those about the base of the rachilla of the spikelets. The description of the hairs, ". . . a tube with somewhat thickened walls . . ., few, if any cross walls, and they terminate in definite points, . . . extremely fragile," suggests this. It is far more likely than that they are "wild fibers from the vascular system." With the exception of some obviously fasciated forms, we have found nothing in the structure of maize for which a homologue could not be found, if not in maize, then in other grasses. All the obvious variations which distinguish tunicate, teopod, corn grass, and *ramosa* maize from the usual plants follow a definite pattern. In the case of structures described as "supernumerary silks from between the rows of grains," for example, these turned out to have a simple explanation. They were silks of partially developed lower flowers of the spikelets.

Glumes are generally smaller in South American highland maize. Not only are they smaller in the common varieties of maize, but in ears which have the tunicate character the enlarged glumes frequently do not cover the grains. This

is in contrast with North American ears which have the tunicate character, for these ears usually have glumes several times longer than the grain. The staminate glumes in South American tunicate plants often are only slightly longer than those of their normal sister plants. While some of the ears we collected might have carried the weak allele of tunicate described by Mangelsdorf (1948), small glumes were common in Dr. Brieger's crosses of pod corn and native South American corns.

While the smaller glumes in South American maize are probably due to several modifiers, there is a dominant gene, vestigial glume, which has been described by Sprague (1939). The original material was a single plant in a small planting of corn from the Belgian Congo. The glumes are greatly reduced, both in ear and tassel. Unfortunately the plant produces very little pollen because the anthers are exposed to the sun. This has made it difficult to produce a commercial sweet corn with the vestigial glume character.

Thick and hard plant parts are most prominent in plants which appear to have some tripsacoid influence, although the glumes and cobs of some Guatemalan Big Butt maize (Anderson & Cutler, 1942) and of Guarani flint from lowland South America are almost as hard as those of teosinte and some *Tripsacum*.

In ears of maize with only a few grains, all parts of the phytomers in which grains develop are hardened and have their usual colors, while the phytomers which do not develop grains are soft, flexible, and lack strong coloration.

LODICULES

Up to now we have been discussing structures which fall outside of the flower. If we consider the pattern for the monocotyledonous flower to be essentially that of the lily, the lodicules represent the remnants of the inner perianth whorl. The outer perianth whorl is absent. Usually only two lodicules are present, although Sharman (1939) has found some spikelets with three. The lodicules in maize, teosinte, *Tripsacum* and *Manisuris* are best seen shortly after the silks emerge or the day the flowers open to release the anthers. At this time the lodicules, which have swelled and thus forced the staminate flower open, are large and turgid. Even though the lodicules no longer function in the maize ear, they still become turgid at the proper time. In some of the highland Bolivian maize the lodicules were exceptionally large and had a definite vascular system.

STAMENS

Usually there are only three stamens in each staminate flower, but occasionally there are none, and sometimes two, four, or five. From their position in reference to the lodicules and to the three carpels, we know that the stamens represent only one, the outer, of two whorls of stamens of our pattern lily flower. In one specimen of maize with four anthers, the extra stamen arose between the two lateral stamens of the normal three and thus appears to represent one developed from the inner whorl of stamens. In the rather frequent staminate maize flowers with only two stamens, the remaining two were the lateral ones.

Although the stamens in the pistillate maize flowers are usually vestigial, they occasionally develop, especially when the plant is grown under peculiar conditions or is influenced by some gene with a strong effect, such as tunicate, or some tassel seed genes.

There is some variation in the diameter, length and shape of cross-section of the filament, but the most conspicuous variations in the stamen are in the anther. Colors vary widely and are related to colors in other parts of the plant. In size the anthers range from occasional minute ones (about 3 mm. long in one of our dwarf Paraguay crosses with Golden Bantam) to nearly 9 mm. (in an exceptional tassel of open-pollinated yellow dent). Most of the paired locules are cylindrical and round off suddenly at the ends but in some the ends are pointed. Although we have not seen anthers like those described as bearing the gene "warty anther" (Emerson, Beadle and Fraser, 1935), partially collapsed and partially functional anthers are common.

The pollen of maize is the largest in the grass family (Wodehouse, 1945) and is twice as large in diameter as wheat pollen. Some of our lowland Bolivian and Paraguayan plants had pollen grains which measured about 60 μ, just slightly larger than the largest wheat pollen, but most maize pollen grains are about 100μ in diameter. Markings on all the grains we examined are quite uniform.

Pollen of plants with the dominant gene, gametophyte factor, fertilizes 95 to 99 per cent of the kernels of plants with the gametophyte factor when it is in competition with pollen lacking the factor. Another gene, small pollen, governs the appearance of pollen that is smaller than usual. There are numerous male-sterille genes, most of them recessive, which control shrivelled or non-exserted anthers and non-functional or abortive pollen.

PISTILS

The three carpels of the grasses under consideration are united into a unilocular, one-seeded ovule. Of the vascular strands in the midribs of the carpels, only those of the two lateral carpels, the ones which do not bear the grain, continue into the style and the two branched hairy stigmas. Occasional plants of *Tripsacum* and maize have three stigmas. In maize the style is very short and the entire silk and the bifurcate tip is stigmatic. The length and thickness of the stigmas and the number and size of hairs on them vary greatly, not only in maize, but also in teosinte, *Tripsacum* and *Manisuris*. The color of the silk in these grasses is, like that of the anthers, related to colors in other parts of the plant.

SUMMARY

1. The grass plant is made up of units called phytomers, which consist of an axillary bud at the lower end, a section of the axis, and a leaf at the upper end.

2. Although the units are modified in the various parts of the plant, their parts are homologous, whether they are in the vegetative or reproductive areas of the plant. Therefore, changes in structure of any part of a unit are often repeated

in the other units. Homologies of the parts in maize, teosinte, *Tripsacum* and *Manisuris* are discussed.

3. A study of homologous variation is of value in plant breeding because it is often possible to identify plants carrying desirable seed characters by a study of the staminate parts or the stem. Plants which will be useful in crosses can be selected at the time pollinations are made.

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We are indebted to the Director of the Chicago Natural History Museum for permission to publish this paper outside of the regular Museum publications. To Dr. F. G. Brieger, Escola Superior de Agricultura, Piracicaba, Brazil, we are grateful for the use of his laboratory and experimental fields while we were in southeastern Brazil, and for the opportunity to study the excellent collection of maize he has assembled and grown during his years in Brazil. Some of our material was gathered while we were working on a joint study of variation in the spikelets of native South American maize, a project which was interrupted by the war. To Dr. William L. Brown, Pioneer Hi-Bred Corn Company, Johnston, Iowa, we are indebted for growing some of our material during several seasons and for specimens of many commercial inbred lines for which he had mapped chromosome knob positions. To Dr. Paul C. Mangelsdorf, Harvard University, we are grateful for his kindness and advice while this material was being collected and studied, and for his loan of many of his collections. We want to thank Dr. Martin Cardenas, Universidad Autonoma Simon Bolivar, Cochabamba, Bolivia, for his help and the use of the University experimental fields while we were in Bolivia; and Dr. Edgar Anderson, Missouri Botanical Garden, for his stimulating suggestions and encouragement. To many others not mentioned we are indebted for the opportunity to study their material in the field and in the laboratory. Part of the South American studies was done while the senior author was a Fellow of the John Simon Guggenheim Memorial Foundation, 1942-3, 1946-7.

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RIGHT-HANDED AND LEFT-HANDED CORN EMBRYOS

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The vertical stem of a corn plant, with its two rows of leaves arranged in a plane, has the appearance of a bilaterally symmetrical structure, but a close examination shows that this appearance is deceptive. The sheath of each leaf of such a plant is wrapped around the internode with its edges overlapping. If the observer imagines himself as standing in the position of the internode of the stem, with the leaf sheath around him like a coat, he will find that sometimes the right half of the sheath overlaps the left, and sometimes the left overlaps the right. For convenience we shall designate the one as dextral, or right-handed, and the other as sinistral, or left-handed. Further examination of the plant reveals that the dextral and sinistral leaves are arranged in alternate sequence along the stem. Thus it follows that the overlapped sides of the sheaths all fall on one side, and, if we should split the plant lengthwise in the plane of the midribs of its leaves, one half would have only the overlapping sides of the sheaths and the other would have only the overlapped sides (pl. 34).

This asymmetry of the shoot, which is characteristic of almost all grasses, is further shown in various species by other characteristics. Usually there is some difference between the two sides of the collar at the top of the sheath; the auricles, when present, ordinarily show some differences and alternately reverse their direction of overlapping in successive leaves; the leaf blade is frequently asymmetrical; and the insertion of the base of the sheath marks a spiral line on the stem. This structural pattern may be regarded as a sort of morphological dorsiventrality, but it is apparently not always correlated with orientation in rhizomes, stolons, or other horizontal stems.

Since the overlapping edge of the sheath is inserted on the stem a little lower than the overlapped side, it follows that the line of insertion of a right-handed leaf describes a left-handed spiral, and that of a left-handed leaf a right-handed spiral. This reversal of direction of the spiral at each node is an aspect of the phenomenon known as *antidromy*, which received much attention, especially from German morphologists, during the latter half of the nineteenth century. It occurs in one way or another in many kinds of plants and has been cited in objection to the theory that the distichous arrangement of the leaves of a grass can be interpreted as a form of spiral phyllotaxy (Elias, 1942, p. 29).

The significance of this reversal of pattern in consecutive phytomers has never been fully explained. As far as the grasses are concerned, it is only a part of a more comprehensive pattern in which various other structural differences appear in successive internodes. In some species, for example, the stem has alternately long and short internodes, the short ones sometimes being so reduced that the leaves appear to be opposite (pl. 34).

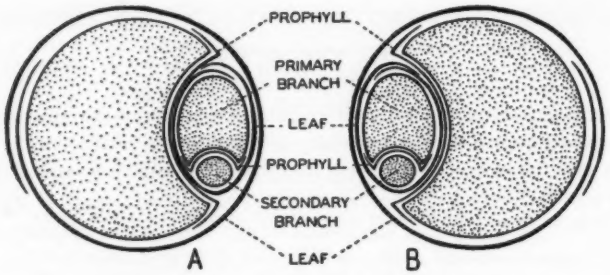

Fig. 1. Cross-sections of two consecutive internodes of a corn stem, showing leaves and axillary structures. A birdseye view of the structural pattern of the plant can be produced by superimposing one of these diagrams on the other. Note that the overlapping edges of the leaf sheaths are both on the same side of the stem and that the secondary branches both fall on the opposite side.

It is obvious that every individual grass seedling must start out in life as either a right-handed or a left-handed plant, as being determined by the direction of the overlap of the sheath of its first foliage leaf, the coleoptile being excluded from consideration. When a large number of embryos of any one species are classified as dextral or sinistral, the ratio is approximately 50:50. This can readily be demonstrated by examining the seedlings grown from a handful of corn.

When a branch arises in the axil of a leaf, its true foliage leaves (the prophyll excluded) fall in a plane which cuts at right angles the plane of the leaves of the main stem (fig. 1). The sheath of the lowest leaf of the axillary branch ordinarily overlaps in the same direction as that shown by the leaf subtending the branch; that is, right-handed branches arise in the axils of right-handed leaves and left-handed branches in the axils of left-handed leaves. To this there are, however, occasional exceptions.

Furthermore, the first leaf of a branch, with whatever axillary structure it may subtend, is located on the side of the branch next to the overlapped side of the subtending leaf of the main axis. From this there may result a peculiar picture in a grass which branches profusely. Suppose we have a vertical grass stem whose leaves stand in an east-west plane, with the overlapped edges of its leaf sheaths all on the south side. In the axil of each leaf there develops a branch, the plane of whose leaves extends north-and-south. Each of these primary branches produces a branch of the next order in the axil of its lowest leaf. All these secondary branches will then fall on the south side of the plant, producing at first a very asymmetrical structure.

This same pattern of asymmetry is carried into the inflorescences of many grasses as far as the branching of the various axes is concerned. Ordinarily nothing comparable with the regularity of the overlapping of leaf sheaths can be detected, for the simple reason that grass inflorescences seldom have bracts sufficiently

developed to overlap. It is generally conceded that at least the glumes and lemmas of the spikelet are reduced leaf sheaths, but they are usually not broad enough to encircle the rachilla and overlap.

Toward the close of the past century a number of interesting cases of antidromy were reported and discussed in a series of papers by George Macloskie (Macloskie, 1895, 1896, 1896a, 1896b). Many of the plants with which he deals are outside the grass family, and I have not examined them, but one observation on the structure of the ear of corn is obviously not plausible, and I have been unable to substantiate it by re-examining the material. The point in question is not one of great consequence, but it does involve an interesting fact. Moveover, Macloskie's statement has been cited in at least one later study (Elias, 1942, p. 29) and will, if not corrected, continue to lead to confusion. A refutation seems, therefore, to be in order.

The problem can best be presented by quoting the following extracts (Macloskie, 1895, pp. 379–380). The italics are mine.

> "It was then shown that . . . . . there must be two kinds of plants of every species of the order [Gramineae]; the one kind or 'caste' has its lowest foliage leaf . . . . . with the right margin of its sheath overlapping the left margin, 'dextrally infolded' as I term it; and the other caste has the left margin overlapping the right, 'sinistrally infolded. . . . . Thus it became manifest that as there are two castes of the maize plant, so there are two castes of grains, the one being the 'antidrom' of the other . . . . . ."
>
> "The ear consists of columns each containing a pair of rows of grains; we may designate the row opposite our right hand as dextral and the other row (opposite our left) as sinistral. It was soon made out that in the particular ear examined *the grains of the dextral row were all with dextral embryos, and those of the sinistral row had sinistral embryos.* Whether this law would apply to all the ears on one plant, or whether the order would be inverted between the ears arising from successive nodes, or between the ears of different plants, is yet to be determined. On examining the very young ear of maize I found the grains of the paired rows of each column oriented close to each other, almost face to face, the young styles running up together, and a gap between the adjoining two-rowed columns.
>
> "From this discovery the inference was obvious that the seeds of corn differ from each other antidromically, *according to the side of the placenta or axis from which they arise; that their embryos vary in consequence, and determine the caste of the future plant.*"

From the above it is obvious, in the first place, that Macloskie was confused in his understanding of the morphology of the ear of corn. A pair of rows of grains is not at all the morphological equivalent of two rows of seeds attached to a linear placenta. Furthermore, on theoretical grounds, I have for many years questioned the accuracy of his observation. Granting that the general antidromic pattern of vegetative structure of a grass plant is as described, there still seemed to be no plausible reason why it should affect the pattern of the embryo. The characteristic pair of grains of corn is borne in two separate spikelets on a short branch arising from the side of the cob. These two spikelets, representing secondary branches on this short primary branch, might be expected to reflect the normal antidromic vegetative pattern even though this be difficult to detect. But why should the pattern continue into the embryos, which are entirely separate morphological entities?

Macloskie seems to have had some misgivings about his thesis and leaves the way open for amendment in the light of further study. As far as I have been able to learn, no later report was ever made. He does not indicate how many pairs of grains he examined, but the number must have been small. Over a period of some five or six years we have from time to time examined individual ears of a dozen or more varieties from widely separated localities, and in not one of them have we found verification of Macloskie's statement. In practically every instance, the examination of only two or three pairs of grains was sufficient to refute it.

In the early studies, the ear selected was held with its tip up, and grains from the left and right rows of a pair were removed and planted separately. The following classification of embryos represents a combination of the results secured from several pairs of rows of a commercial dent variety. It is typical of the results from several ears studied in this way.

Sinistral embryos in grains from left row	114
Dextral embryos in grains from right row	128
Dextral embryos in grains from left row	121
Sinistral embryos in grains from right row	111

It will be noted that only those embryos of the first and second categories, approximately 50 per cent of the total number, conform with Macloskie's statement. The other two classes should not have occurred at all.

But the error as to the structural pattern of the individual *pair of spikelets* is really greater than indicated above. This is disclosed by a comparison of the right and left grains of individual pairs. Paired grains were planted side by side, and the paired seedlings fell into the following classification:

Pairs with left embryo sinistral and right dextral	95
Pairs with both embryos dextral	130
Pairs with both embryos sinistral	95
Pairs with left embryo dextral and right sinistral	104

Of these four classes, only the first, approximately 25 per cent of the total number, conform with Macloskie's statement. The second and third classes may be said to be half right as far as individual grains are concerned, but wrong as an expression of the pattern of the pair. The third class is entirely wrong.

From these observations it is evident that the type of embryo—sinistral or dextral—is determined solely by chance. It is in no way correlated with the position of the grain in the typical pair of spikelets.

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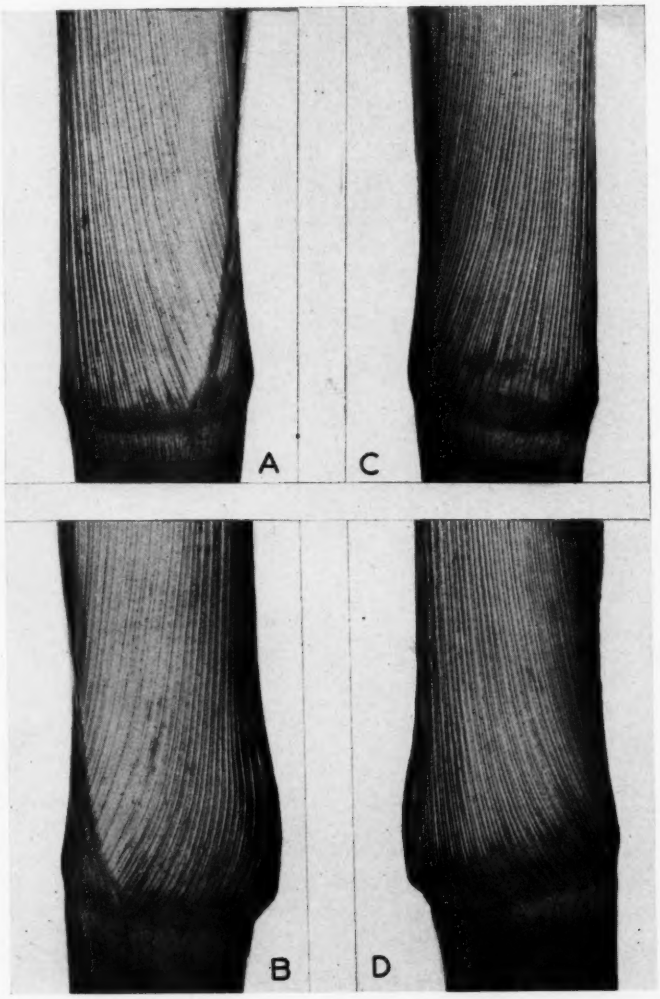

WEATHERWAX—RIGHT- AND LEFT-HANDED CORN

Fig. 2. *A* and *B*, two consecutive nodes of a corn plant, as seen from the same side of the stem. Note that in *A*, the left side of the sheath overlaps the right, and that in *B* the overlap is in the opposite direction. In *C* and *D*, the same nodes are shown from the other side of the stem.

3

4

WAXY—RIGHT—AND LEFT-HANDED CORN

Explanation of Plate

PLATE 35

Fig. 3. Part of a plant of St. Augustine grass *(Stenotaphrum)*. The appearance of opposite leaves and opposite branches, which is unusual in grasses, is due to the alternate sequence of long and very short internodes in the stem.

Fig. 4. Paired grains on an ear of corn. In *A* the paired rows of grains are connected by the curved lines at the top. *B* and *C* show pairs of grains from the upper and lower sides, respectively. Since the two spikelets which produce the pairs of grains are consecutive lateral branches on a short primary branch, *they* might be expected to show antidromical patterns, but there is no reason why such patterns should extend into the embryos of the grains. Examination of the embryos shows that their pattern is determined by chance and not by the position of the grain in the pair of spikelets.

A MORPHOLOGICAL ANALYSIS OF ROW NUMBER IN MAIZE

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The kernels of an ear of maize are usually set in longitudinal rows of from 8 to 30 or more. Certain genetic stocks, and an occasional ear in open-pollinated varieties, may have only 4 rows. For numbers much above 30, the kernels are so crowded that the rowing is obscure; various irregularities may modify or conceal the row pattern (Weatherwax, 1916, 1917), but in most of the varieties of *Zea Mays* the kernels over a good portion of the ear are arranged in definite and usually conspicuous rows. In nearly all varieties the row number is even, since the kernels arise from paired spikelets which are themselves disposed in regular rows (Collins, 1919).

The history of row number is apparently complex. Both in South America and in the southwestern United States archaeological investigation has demonstrated that the earliest varieties had 12 or 14 rows (Bird and Anderson, in press), and Bird's recent excavations indicate that this condition persisted unchanged for a long period. Both in South America and in the southwest 8- and 10-rowed varieties appeared at a later date (Carter and Anderson, 1945). Another type of change in row number has been associated with the dent corns of Mexico. Since at least the times of the Toltecs, row numbers of 16 and above have been characteristic of central Mexico (Anderson, 1946), and it is apparently chiefly from that center that they have been so widely spread around the world as to characterize many of the world's centers of commercial corn production.

Since the early days of studies upon inheritance in *Zea Mays* (Emerson and East, 1913) it has been apparent that the genetic basis for differences in row number is complex. Extensive and careful studies were carried on by the late R. A. Emerson and his students and collaborators for several decades. While he made a number of preliminary and informal reports his results in different crosses were rather contradictory and have not yet been formally published. Lindstrom (1929, 1931) observed linkage between genes for row number and genes for pericarp color.

The morphological bases for differences in row number are difficult to study upon the ear itself, an organ so modified that its exact relation to other grass inflorescences is still a subject for research and so highly vascularized that such research is technically difficult. Accordingly, for the past decade, we have carried on a comprehensive survey of variation in both the ear *and* the tassel (the male and female inflorescences). As Bonnett's (1940) developmental studies have clearly shown, these two inflorescences are scarcely distinguishable morphologically in their early stages but beyond a certain point the ear becomes progressively harder and thicker, the tassel progressively more lax and expanded. From modern

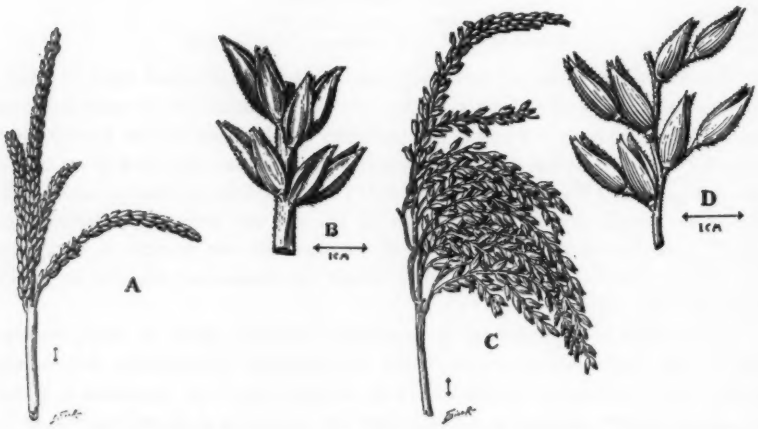

Fig. 1. Two extreme tassel types from an inbred plot. *A* and *C* show the general habit of the tassel. A few branches have been removed from *C* as indicated in the drawing, to reveal the structure of the tassel. *B* and *D* show equivalent portions of the lowest tassel branch from *A* and *C*. The arrow under the figures is 1 cm. in length. Condensation in *B* is 2.0, in *D*, 1.0.

genetic theory we know that the germinal differences between various types of ears will also be operating in the tassels of those same plants. Since the tassel is an expanded and relatively unmodified organ, changes which are difficult to determine and equally difficult to interpret when viewed only in the ear are easier to score and simpler to understand when studied in the tassel. Therefore, though this paper is primarily an attempt to analyze variation in the ear, we must first consider the morphology of the tassel with reference to its pattern of variation.

Though the tassel (like all other parts of the corn plant) varies greatly from one strain to another, its basic plan is singularly uniform. It is composed of a central axis with a varying number of secondary branches, terminated by a dense portion which has generally been referred to as the central spike. The secondary branches may themselves be branched, particularly the lower ones, and in some kinds of maize there may even be branching of the fourth and fifth order.

The fundamental unit of the tassel is the spikelet, technically a condensed raceme. It is about a centimeter long and has two chaffy basal glumes which cover and conceal the remainder of the spikelet except for a short period during anthesis. In *Zea* the spikelets of the tassel are almost universally borne in pairs, one of which is practically sessile, the other being noticeably (and oftentimes conspicuously) pedicellate (fig. 1). This condition characterizes not only *Zea*

but nearly all of the genera in the two tribes of grasses (Maydeae and Andropogoneae) with which this genus is obviously most closely related.

In modern maize one of the most conspicuous variables in tassel structure is the arrangement of the spikelet pairs. In the wild grasses related to maize these arise one pair at each node, and in South America and in the Orient there are wide areas in which all the varieties of maize are so characterized. In the maize of central Mexico, however, this fundamental pattern has been so greatly altered as to be almost unrecognizable in its extreme manifestations. Since it was apparently from this center that most of the dent corns of commerce were ultimately derived, these same anomalies, in a somewhat diluted form, are to be found in all the areas of commercial corn production where dent corns play a dominant role.

Superficially, the Mexican dents (and associated rice popcorns) are characterized by compact, clubby tassels, densely set with spikelets. This condensation is equally true of the central spike, and of all the secondary and tertiary branches. When the spikelet arrangement on the secondary branches is examined in detail, it is evident that the dense effect is due to a kind of fasciation or telescoping of successive nodes. This telescoping may be of various intensities. In some commercial United States varieties it affects only a portion of the nodes. In such varieties the majority of the nodes will bear a single pair of spikelets, but a few may have two or more pairs. The most extreme manifestations of this tendency are seen in such kinds of maize as the short-eared many-rowed dents from central Mexico to which Anderson and Cutler (1942) have given the name of Mexican Pyramidal, and in the closely related rice popcorns such as Japanese Hull-less. In these varieties there may be no normal nodes along the whole length of the tassel branch, and the average number of spikelet pairs per apparent node may be four or five. (We say apparent node since there are various reasons for believing that the node number itself has not been primarily affected and that the peculiarities of these kinds of maize are due to a telescoping of successive internodes so that what seems to be but a single node with several pairs of spikelets is in reality a succession of nodes virtually on top of each other, each with its own pair of spikelets.)

This telescoping of the inflorescence has been designated as "condensation" (Anderson, 1944). Its effect can be seen throughout the tassel and it might conceivably be measured in the central spike, or on all or on one of the secondary tassel branches. Experience has shown that the most consistent results are obtained when it is scored on the lowermost secondary branch. (When, as in certain inbred strains, the lowest tassel branch is manifestly malformed, the next branch above is chosen for scoring.) Condensation is scored by recording for the central portion of the branch the ratio between the number of pairs of spikelets and the number of apparent nodes. (For precise directions see Anderson, 1944). This ratio runs from 1.0 in the uncondensed varieties of South America and of the Orient, to 4.0 and higher in Mexican dents and in certain inbred lines which resemble them.

As soon as the phenomenon of condensation had been recognized it was obvious that there was a close connection between condensation of the tassel and high row numbers of the ear. All maize varieties with row numbers of 16 or above were, without exception, found to exhibit condensation in the tassel. Eight-rowed varieties, without exception, were found to have no condensation. By utilizing inbred lines to minimize the effects of environmental variation it was possible to demonstrate that the over-all relation between row number in the ear and condensation of the tassel is so exact that it may be expressed in a mathematical equation. If we let C represent the condensation ratio, and R the number of rows on the ear, then these two variables are related in the following way:

$$R = 10C.$$

The relationship has been tested with a wide variety of material,—United States open-pollinated varieties, inbred lines derived from these varieties, Mexican varieties, Guatemalan varieties, popcorns, sweet corns, etc. The exactness of the correlation depends upon the variability of the stock which is being examined. If, as in the original investigation, one grows twenty or more plants of various inbred lines under optimum conditions, choosing a characteristic tassel from each inbred line, and a well-developed ear, then the correlation will be very high. There are a very few inbreds in which condensation of the tassel is not accompanied by a corresponding increase in row number, but they are very much in the minority as fig. 2 demonstrates. If open-pollinated maize is grown, two or three plants to a hill, and then the condensation of each tassel is correlated with the row number of each ear, the correlation is quite naturally less exact, but it is still clearly demonstrable.

In the commercial dent varieties of the United States there is an interesting variation in this correlation which has a logical basis. In Mexico the relationship between condensation and row number approaches a simple straight-line (Wellhausen, Roberts and Lenz). In United States dents the relationships between these two variables is curvilinear as shown in fig. 2. In other words, in North American maize a tassel may indicate an exceedingly high degree of condensation, yet the row numbers will be only in the lower 20's instead of in the 30's. This is probably due to the intense selection for ears of 18 to 22 rows which took place for several decades under the influence of the corn shows. The corn-show ideal called for an ear of 18 to 22 rows, but discriminated highly against ears with higher row numbers. During this period modifying genes which would have held down the expression of high condensation in the ear would have been at a selective advantage. The differences between scatter diagrams for tassel condensation vs. row number in Mexico and in the United States suggest that such modifiers are common in United States varieties. Further evidence for such modifiers was obtained from crosses between the two common inbred lines, WF-9 and 38-11, with Japanese Hull-less popcorn, a variety with a very high row number and extreme condensation. F-2's of 125 plants each were grown and scored for row number

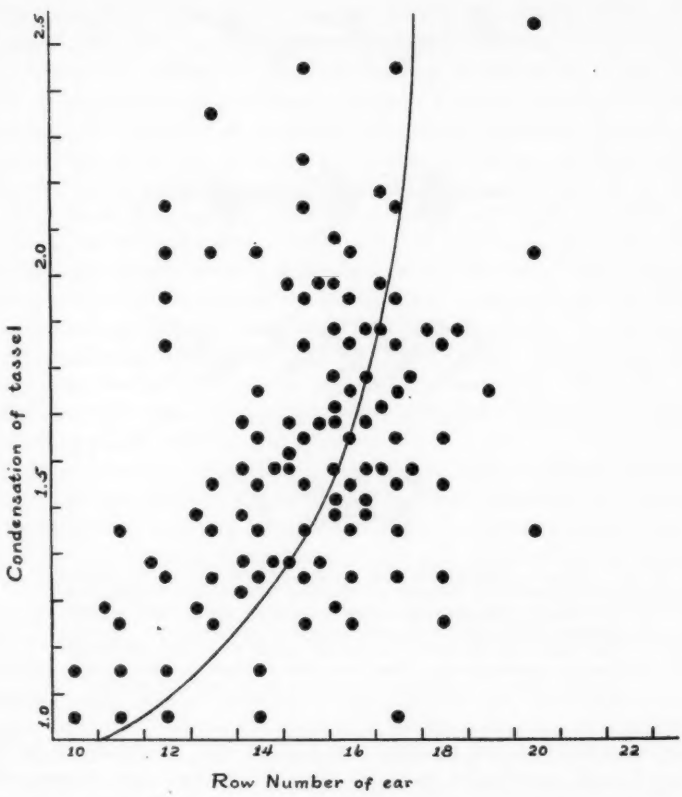

Fig. 2. Scatter diagram showing relationship between condensation and row number in 109 inbred lines. Condensation was scored on three tassels and averaged. Row number is the average of all the plants bearing well-developed ears (usually about 10.)

of the ear and condensation of the tassel. In each cross, row number of the ear and condensation were strongly correlated but extreme condensation of the tassel was not accompanied by row numbers of 30 or 40 as in the popcorn. Furthermore, this restricted expression of condensation was stronger in the cross with WF-9 than in that with 38-11. It was even greater in an F-2 between 38-11 and WF-9 than in the crosses with Japanese Hull-less. These results indicate that corn-belt maize does carry modifying genes which hold down the expression of condensation in the ear and that there are more such modifiers in WF-9 than in 38-11.

If condensation of the tassel is to be used as a precise indication of row-number potentiality, it must, however, be carefully determined. Since the first paper

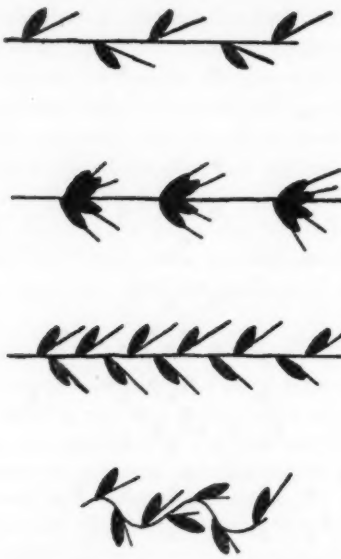

Fig. 3. Diagram showing various arrangements of the spikelet pairs on secondary branches of the tassel. In all four diagrams only the pedicel of the pedicellate spikelet is shown. From above to below: normal; highly condensed; short internodes; spiralled axis. Although the lower two produce thick-looking tassels which are superficially similar to those with condensation, their thickness is due to fundamentally different phenomena and has no effect upon row number.

(Anderson, 1944) on this subject some workers have attempted to lessen the tedium of tassel examination node by node. They have instead measured the density of the tassel in some such way as number of spikelets per centimeter of length. Though condensation does indeed produce a dense tassel, there are numerous other variables which may produce dense tassels without affecting the row number, as, for instance, short internodes or a spiraled axis (fig. 3). While it is true that after one understands the effects of condensation he can often estimate the row potentialities by merely glancing at a tassel in the field, it is equally true that in any precise investigation of the phenomenon it must be accurately determined according to the original directions.

Another abnormality of the inflorescence which affects row number has been described as "multiplication" by Cutler (1946). It apparently causes the bifurcation of the spikelet at a very early developmental stage so that two spikelets are produced instead of one. A high degree of multiplication is difficult to distinguish from a high degree of condensation, but lower grades are readily distinguishable in the tassel. In condensation the spikelet pairs tend to be regular, but successive pairs are arranged practically on top of each other. In multiplica-

tion the arrangement is normal but either or both of the spikelets within the pair is doubled. The effects are also different on the ear. Condensation produces ears in which the row rumber has been increased but in which the rowing is still regular. Multiplication adds additional kernels in a more or less crowded irregular fashion until the regularity of the rowing is no longer apparent. Extreme multiplication is rare in the United States and in Mexico, common in certain kinds of Guatemalan maize, particularly the yellow flints of the mountains, and is common in parts of South America. Its expression is most readily studied in what would otherwise be an 8-rowed variety. With a little multiplication there are occasional diamond-shaped kernels squeezed in between the regular rows. This is a common condition in flints of the northeastern United States. With a further development of the phenomenon there are so many of these extra kernels that the ear is divided into four quadrants, each representing two original rows. Within each of these quadrants the rowing is difficult or impossible to make out. With still further multiplication, the entire ear is so crowded with kernels that it can no longer be considered to possess a definite row number.

In the earliest stages of our investigation Dr. G. Ledyard Stebbins pointed out, from his wide knowledge of the Gramineae, that such phenomena as condensation and multiplication represent obvious teratological variations which have been selected under cultivation because they increase the row number and hence the productivity of the crop. Continued study has confirmed the soundness of his judgment. Nothing like either multiplication or condensation is characteristic of any of the wild-growing Gramineae. Furthermore, the extreme manifestations of condensation, such as are seen in certain inbreds or in an occasional ear from an open-pollinated variety of dent corn, are clearly fasciated. In the prehistoric remains of maize from the American southwest these fasciated extremes seem to have been more frequent when highly condensed varieties were first introduced into that area than they now are. This would suggest that the condensed varieties have gradually accumulated a set of modifiers which allow condensation to increase row number but tend to prevent the production of extreme, fasciated ears.

Therefore, if we are to study the variation pattern of the central spike, it would seem a good working hypothesis to confine our attention to varieties which are without either condensation or multiplication. It is clear that condensation affects this part of the tassel but it produces such thickly set spikelets that all other variation is obscured. To understand the basic variables one must concentrate upon non-teratological strains; in other words, upon maize which is without either condensation or multiplication.

VARIATION IN NON-TERATOLOGICAL MAIZE

If in this way we exclude the effects of condensation and multiplication, variation in the central spike is simple. All of the maize we have examined then falls in two extreme classes and intermediates between them. The 8-rowed varieties have the spikelet pairs of their central spikes in whorls of two. The 12-

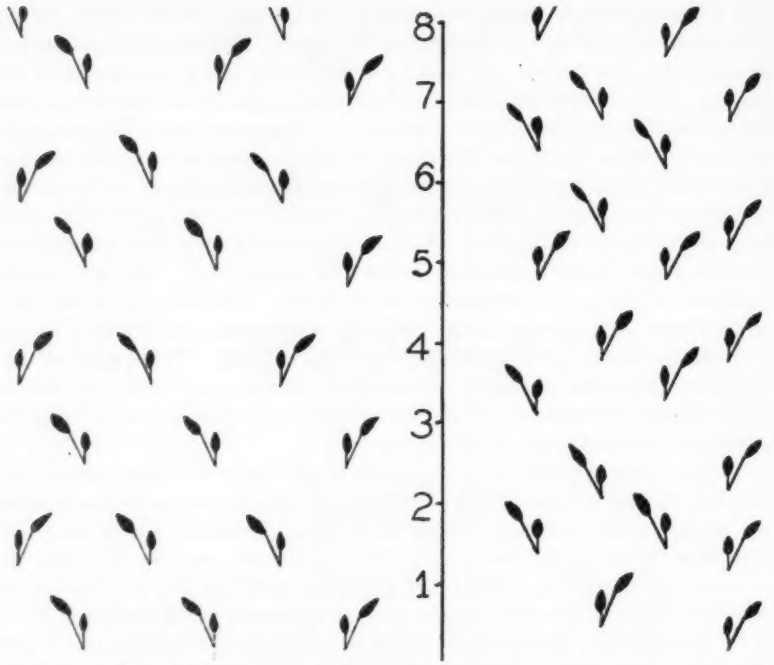

Fig. 4. Measured diagram showing spikelet arrangement in 8-cm. portions of two central spikes. Left, from a 12-rowed flour corn from the Southwest. Right, from an 8-rowed northern flint. Scale in cms. Further explanation in the text.

rowed varieties have their spikelet pairs in whorls of three. In the 8-rowed varieties, as for instance in the older varieties of flints of the northern United States, the spikelet pairs are opposite and decussate. That is, if the pairs at any one node are set east and west, those at the next node are north and south, then the next pairs east and west, etc. Looking down the spike from the apex there will be spikelet pairs on four sides of the central spike, making 8 rows in all. The 8-rowed ear has an 8-rowed central spike.

Similarly in 12-rowed varieties without condensation or multiplication, if the whorl of 3 pairs at any one node is represented by positions 2, 6 and 10 on the face of a clock, then at the next node we shall find positions 12, 4 and 8, then 2, 6, 10 again, and so on. Looking down the central spike from the apex we shall see spikelet pairs on six of its sides, making 12 rows of spikelets. The plant with a 12-rowed ear has a 12-rowed central spike to its tassel. The complete homology between the two organs is as simple as that. Figures 4 to 6 show spikelet positions as actually measured on representative central spikes. The measuring was done according to the method originated by Mangelsdorf (1945) but the results have

been plotted on a scale of approximately equal value horizontally as well as vertically. The central spikes were examined under a dissecting microscope with a wide field. Accuracy was increased by having an assistant record the measurements. Several centimeters of the spike (usually a half to a third of its entire length) were chosen for examination. A mark is made with dye or ink at the precise spot where the measurements begin. The distance from each spikelet pair to this base line is recorded in millimeters, using a steel rule or calipers. Any one of the pairs at the base is chosen to begin with, and all the pairs which are on the same side of the spike are recorded in succession up the spike, removing each pair as it is measured. In some varieties there are ridges on the rachis which make it a simple matter to follow any one rank of the spike. In others the relationship is obscured, and one has more or less arbitrarily to choose a line of spikelet pairs. These pairs are then plotted to scale on cross-ruled paper, and successive vertical ranks to the right and the left of the original rank are measured until no spikelets remain on the portion of the spike chosen for study. The resulting graph is essentially a cylinder which has been cut down one side and flattened out into one plane. In attempting to make such an examination it is best not to begin with the more complicated types. An 8-rowed sweet corn or a northeastern flint will demonstrate how simple the arrangement can be and experience with it will aid one in interpreting the more complicated spikes of the dent corns.

Figure 4 demonstrates that, in the strict sense of the word, the arrangement of the spikelet pairs on the central spike is not in spirals as has been so frequently reported (as, for instance, in our own earlier papers on the subject). The pairs are clearly in whorls. In 8-rowed varieties they are in whorls of two, in 12-rowed varieties in whorls of three. In both of these sorts there is a regular alternation of whorl position so that the spikelet pairs can be followed in regular spirals in either direction, but this is not a spiral arrangement in the strictest sense. It is condensation which has obscured the simplicity of this regular whorling. With a low degree of condensation the whorling can still be made out from the scaled diagram though it is often difficult to determine from inspection. With a higher degree of condensation, the spikelet pairs are so thickly set upon the central spike that it is difficult or impossible, even from the diagram, to determine what the fundamental pattern may have been.

THE DETERMINANTS OF ROW NUMBER IN THE MAIZE OF THE UNITED STATES

Condensation and number of spikelet pairs per whorl are therefore the two main variables which determine row number in the maize of the United States. Multiplication, particularly in its lower grades, is occasionally met with, but it plays nowhere near the role it does in Guatemala or in South America. Since it may lead to irregular rowing and since the commercial varieties of the United States have been very strongly selected for straight rows, it is possible that its frequency may have been greatly reduced by this intense selection.

Figure 5 demonstrates how number of spikelet pairs per whorl and condensation interact in determining row number in the maize of the United States. Condensation is diagrammed on the vertical axis from the grade of 1.0, where there is no condensation and there is merely the normal pair of spikelets at each node, to the grade of 3.0, where there are on the average three spikelet pairs at each node. The horizontal axis shows the fundamental whorling of the central spike (and therefore of the ear as well) from whorls of two pairs at each node through various intermediate stages to whorls of three at every node. The numbers on the Cartesian surface show the row numbers to be expected with various combinations of these two tendencies.

For the interpretation of row number and particularly for its genetic analysis the most important fact demonstrated in fig. 5 is that for row numbers above 8 there are two quite different kinds of plants which can yield any row number. Take 12 rows, for example. They are to be expected on a plant with no condensation and with a central spike in whorls of three. They are equally likely on a

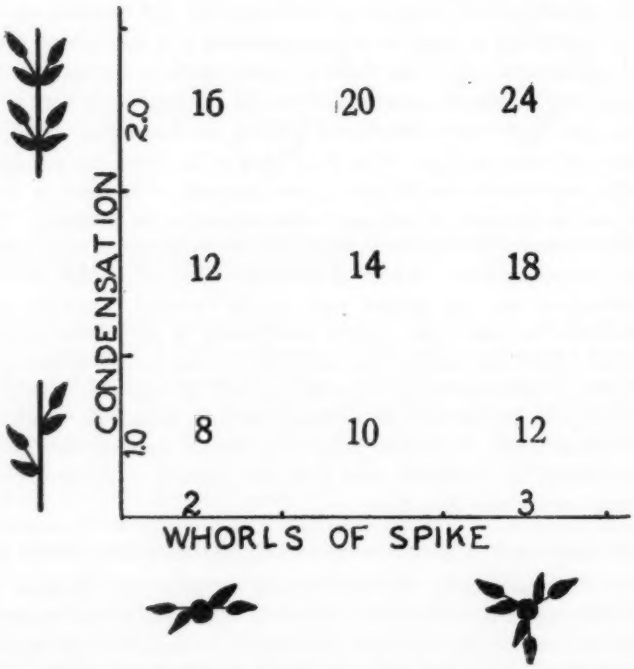

Fig. 5. Diagram showing how whorling and condensation interact in affecting row number. Whorling, from whorls of 2 pairs to whorls of 3 shown on the horizontal axis. Condensation from 1.0 to 2.0 shown on vertical axis. Numbers in the center show row numbers to be expected in the absence of modifying factors or other phenomena such as multiplication.

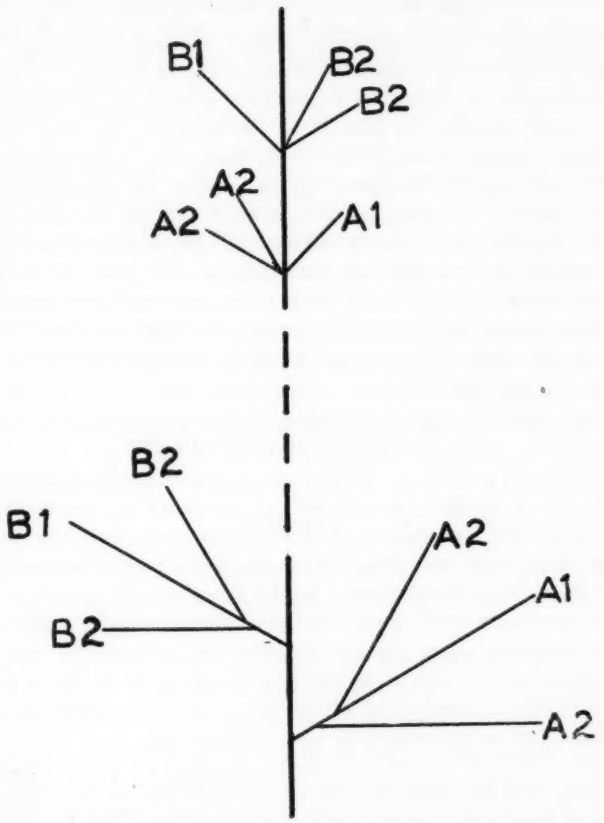

Fig. 6. Diagram illustrating possible relationship between the distichously arranged lower branches of a maize tassel and the whorled upper branches and central spike. Two lower branches are shown, each with its own axillary branches. At the upper nodes two such branches would be represented by two whorls of three. Each whorl takes the place of a primary branch and its two axillaries.

plant with whorls of two but with condensation of grade 1.5. Furthermore, these two types could be distinguished by examining their tassels. In the first type the arrangement of spikelets would be regular throughout, and the central spike would be in whorls of three. In the second type about half the nodes on the lowest secondary branch would have an extra pair of spikelets. The whorls of the central spike would be in two's, somewhat obscured by the disturbance of the spikelet pattern brought about by condensation.

THE INHERITANCE OF ROW NUMBER

The completion of the morphological analysis outlined above makes it possible to proceed with the genetic analysis of differences in row number. It demonstrates, however, the futility of attempting to study the genetics of row number as such. We must instead consider the genetics of condensation *and* whorl number *and* multiplication. Genetic investigations along these lines are already under way. The results now available, though not precise, suggest the general nature of the genetic background. Condensation is apparently due to one or two recessive genes with a considerable number of factors modifying its expression. Differences in whorl number are apparently due to at least several genes; the problem is a complex one. In an 8-rowed variety or in a 12-rowed variety the correspondence between whorl numbers in the tassel and in the ear are absolute. In crosses between such varieties, thresholds of expression may differ in different parts of the tassel and between the tassel and the ear.

THE BEARING OF THESE EXPERIMENTS UPON THE GENETIC ANALYSIS OF MULTIPLE-FACTOR CHARACTERS

Few branches of genetics are of more practical or theoretical significance than those which deal with the inheritance of multiple-factor characters. Yet in this field of genetics little fundamental advance has been made since East first demonstrated that the problem could be brought in line with a single-factor analysis. Row number in maize is such a problem. As the above analysis shows it cannot be understood genetically until it is understood morphologically. Now that we understand something about the morphological and physiological apparatus by which increases in row number are achieved, we are ready to plan a genetic experiment in which the number and distribution of genes responsible for row number differences may be determined, at least approximately.

To work effectively in such problems, one must, in other words, precede genetic analysis with morphological analysis. In a problem of this complexity, the morphological analysis is in itself a subject for research. This is equally true in most other investigations of multiple-factor characters. The general neglect of the morphological bases of such characters is one of the reasons the subject has progressed so little in the last thirty years.

THE ANATOMICAL INTERPRETATION OF THE EAR AND TASSEL

The inflorescences of *Zea Mays* have proved notoriously difficult to explain in terms of classical morphology. Weatherwax (1935) has pointed out that they share with certain other grasses a tendency to be whorled rather than distichous. That does not, however, solve the fundamental difficulty in interpretation. Why should the lower branches of a maize tassel be distichous and the upper branches spiraled or whorled? The facts reported above suggest an explanation. If we confine our attention to non-teratological inflorescences, the typical tassel has distichously arranged branches at its base, then passes through a zone difficult to interpret exactly and has whorls of spikelet pairs all along its upper portion.

Furthermore, these whorls alternate in an exact fashion between two clearly opposite types. If the whorls are of two pairs, for instance, the arrangement is decussate. The distichous branches at the base and the alternation of oppositely arranged whorls at the apex suggest that the tassel is fundamentally distichous throughout and that in the upper part of the tassel each branch has been reduced to a whorl of two or three spikelet pairs as the case may be. The intermediate zone would then be the region in which the reduction of a tassel branch to a whorl of branches has been only partially accomplished.

One argument in favor of this interpretation is that the uppermost tassel branches, those just below the central spike, are themselves clearly whorled, usually for one node and sometimes for two or more. On the view expressed above each of these whorls of two or three branches would represent one branch with its own branchlets condensed upon the main axis, as illustrated in fig. 6. Whorls of two would represent a branch with one branchlet, whorls of three a branch with two. It is perhaps significant that the northern flint corns which are almost universally decussate in their central spikes are also characterized by lower branches which have but a single branchlet.

SUMMARY

1. The problem of row number in maize was studied in the tassel as well as in the ear, the former organ being more accessible for study and its variation being more readily interpreted.

2. One of the chief variables in maize is "condensation," a telescoping of successive internodes. It operates throughout the tassel and the ear but is most effectively measured in the lowermost secondary branch of the tassel. When precisely scored it is directly related to row number by the equation $C = 10\ R$. In United States maize this relationship is less exact above 20 rows, probably due to the intensive selection against varieties with more than that row number during the corn show era.

3. If we rule out those varieties of maize with condensation and multiplication as being teratological abnormalities, then all the remaining varieties have central spikes (and ears) with spikelets in whorls rather than in spirals as has been so frequently reported. Eight-rowed varieties such as the northern flints are in whorls of two; 12-rowed varieties are in whorls of three.

4. The genetics of row number is therefore most effectively studied not as the genetics of row number as such, but as the genetics of condensation, multiplication, and whorl number. Preliminary results indicate that condensation is a simple recessive and that the genetics of whorl number differences is complex.

5. Two problems are discussed in the light of these results: The genetics of multiple-factor characters, and the anatomical interpretation of the ear and tassel.

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THE VASCULAR ANATOMY OF THE FOUR-ROWED EAR OF CORN

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The question of row number eventually arises in any complete study of the ear of corn. It is likely to become involved especially when the origin of the ear is considered. Several years ago the late Dr. R. A. Emerson was growing certain strains of corn in a study of row inheritance. He obtained several ears with four rows from some of the crosses and these were made available to the writer for anatomical study. The immediate ancestry of the plants which produced these ears is not known.

METHODS AND MATERIALS

The same general methods were employed for the examination of the internal anatomy of these 4-rowed ears as were used for the 8-rowed ear.[1] The ears were studied when mature in size but sufficiently soft so that, without embedding and further treatment, serial sections of 160 μ could be made. No staining was necessary to distinguish the vascular bundles when sections were mounted in glycerin. In addition to cross-sections, retted material was used to aid in getting a three-dimensional picture.

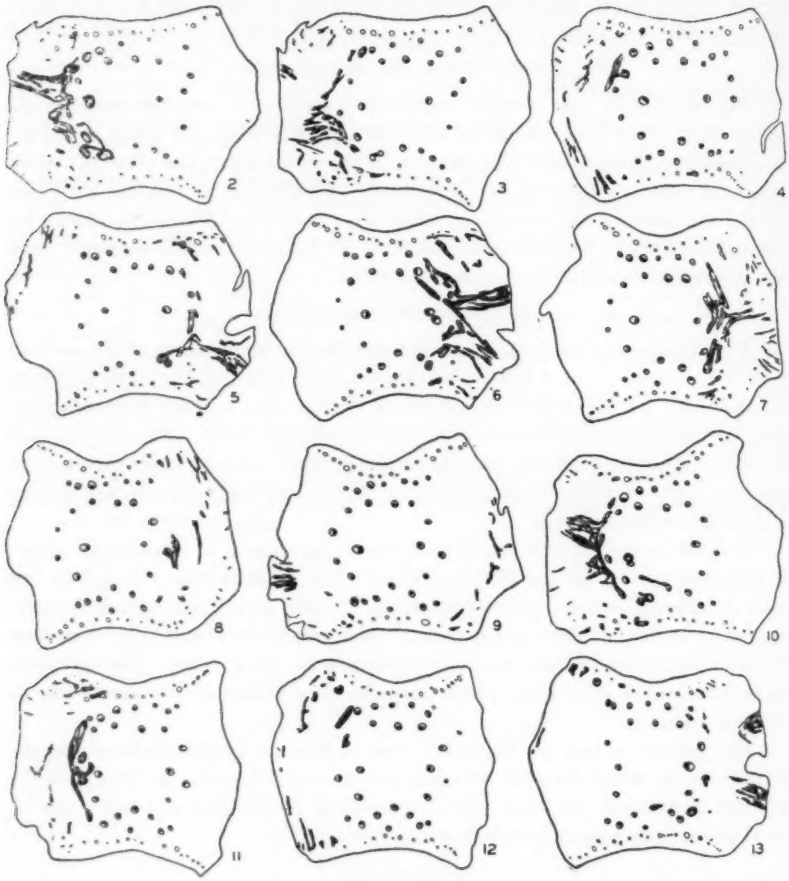
The ears examined conformed in external appearance to descriptions which have already been given for this type of ear. The spikelets were arranged in two pairs of rows opposite each other (pl. 36, fig. 1), thus giving a rectangular appearance in cross-section. Between the pairs of rows were smooth faces. Had these been 8-rowed ears, pairs of rows would have formed on these faces. The specimens showed occasional extra kernels indicating the development of the second flowers of some spikelets.

The general pattern of description used is that previously employed for the 8-rowed ear to which frequent reference will be made. In order to distinguish the vascular bundles of the inner and outer systems in the diagrams more readily, those of the inner system have been partially blocked in.

DESCRIPTION

The change in number, the size, and the arrangement of the bundles in the transition region from the shank to the ear could not be made since the specimens had been collected without the shanks. All indications were that it was essentially like that of the 8-rowed ear previously discussed. The diagrams used in the description represent a part of a series of cross-sections cut about halfway up the ear and extending about four nodes (assuming that each pair of spikelets represents a node) acropetally. The staggering of the pairs of spikelets on the opposite sides aided in interpretation.

[1] Laubengayer, R. A. Paper in press.



Figs. 2–13. Diagrams representing a part of series of cross-sections extending about four nodes.

There is a distinct inner system of bundles—those that are partially blocked in—which contribute to the vascular supplies of the pairs of spikelets along one side (fig. 2). This supply formation is essentially as it is in the 8-rowed ear. It is evident from figs. 3 and 4 that with the passing out of the main spikelet supplies, the bundles again reorganize in their previous relative positions. At the next higher level, the bundle complex on the opposite side is forming the next higher spikelet supplies (fig. 5). This is obviously a repetition of the reorganization of the vascular system at the lower level. The inner system at the level of fig. 9 is shown in its entirety without any spikelet supplies. From the level indicated in

fig. 10 through that shown in fig. 11, the supplies to the next higher pairs are indicated. Thus, there is a very uniform sequence of vascular supply formation acropetally.

It is obvious that the bundle organization is much like that in the 8-rowed ear, as seen by the inner system at the level indicated in fig. 9. If the courses of the median bundles along the smooth faces are followed, it is seen that these are not involved in contribution to the spikelet supplies. This was found to be true in all ears studied except in a single small one. In this one, all bundles of the inner system contributed to the spikelet supplies. Bundles facing the smooth side also contribute in the formation of the spikelet supplies. Hence the system of vascular bundles contributing to the supply of the spikelets is far more extensive laterally than was evident in the 8-rowed ear.

The outer system of bundles is likewise more extensive than was observed to occur in the 8-rowed. As seen in all the figures, the bundles are arranged across the sides without spikelets, with a greater concentration at the corners which are directly associated with the supplies to the glumes (figs. 3–5 and 7–9). There is a lateral anastomosing of these same corner bundles between the levels at which the spikelet supplies leave the axis. This anastomosing gives complete continuity of the bundles of this outer system across the sides bearing spikelets.

A number of bundles of this outer system along the smooth side do not enter into the supplies to any parts. They run the entire length of the ear with little lateral fusion. Thus along the smooth face, there is at least one of the bundles of the inner system and a number of the outer system which run the length of the ear without supplying any organs.

As an aid in the interpretation of these systems, the retted material as shown in pl. 36, fig. 14 helps considerably. Not only do the vascular supplies to the glumes stand out in definite profile, but the remainder of the vascular bundles of the outer system show clearly across the smooth face. Bundles of the inner system can be seen plainly even though they lie below the outer.

DISCUSSION

The anatomical structure of the 4-rowed ear shows a striking similarity in structure with that of the 8-rowed. That there are present two distinct systems of vascular tissue cannot be emphasized too strongly. Paralleling the condition in the 8-rowed ear, the stronger inner system furnishes the main supplies to the paired spikelets. These supplies are formed over a very short distance vertically and pass out almost at right angles into the spikelet axes. In contrast to the condition present in the 8-rowed ear, the bundle complex involved in the supply to the spikelets is greater in circumference so that the total bundle supply is greater than in the 8-rowed. However, there are usually some bundles which do not enter into these supplies—those always on the sides that bear no spikelets. Only in one small ear examined were all the bundles associated with spikelet supplies.

The outer system is relatively stronger than that in the 8-rowed ear. At the margins of the faces which bear the spikelets, the smaller bundles behave in the same fashion as in the 8-rowed. They furnish the complete vascular supply to the two glumes of each spikelet, completely independent of the outer system. Between the levels at which the main supplies to the spikelets pass out, they form complete lateral connections. The presence of bundles of this system offers an unusual condition on the two sides along which there are no spikelets. These bundles show very little lateral fusion and extend the entire length of the ear. They were in no way connected with the supply to any structure in the specimens studied.

The presence, along the two smooth sides of the ear, of parts of the inner system and outer system is significant. From a physiological standpoint, there is far greater proportion of vascular tissue present than would usually be present to supply such an amount of tissue. It is generally accepted that in all groups of plants there are forms which show relatively large amounts of vascular tissue supplying comparatively small masses of tissue. This is usually interpreted as evidence of reduction; the loss of an organ or organs often is completed before the disappearance or radical modification of the vascular tissue supplying these organs. The vascular tissue represents a conservative portion of the plant body and therefore responds more slowly to change in conditions. If this is true in the case of the 4-rowed corn ears, then the present 4-rowed condition is a derived one. Hence it would not represent a primitive condition—if one uses the number of paired rows as a criterion—but a more advanced one; a simpler condition derived from a more complex one. This would be in keeping with the interpretation of similar structures found in other plants. If this is true in the 4-rowed ears, it may be that similar reductions may exist in the higher-rowed ears, with internal evidence. This might well necessitate a general change in the interpretation of the row number of the corn ear.

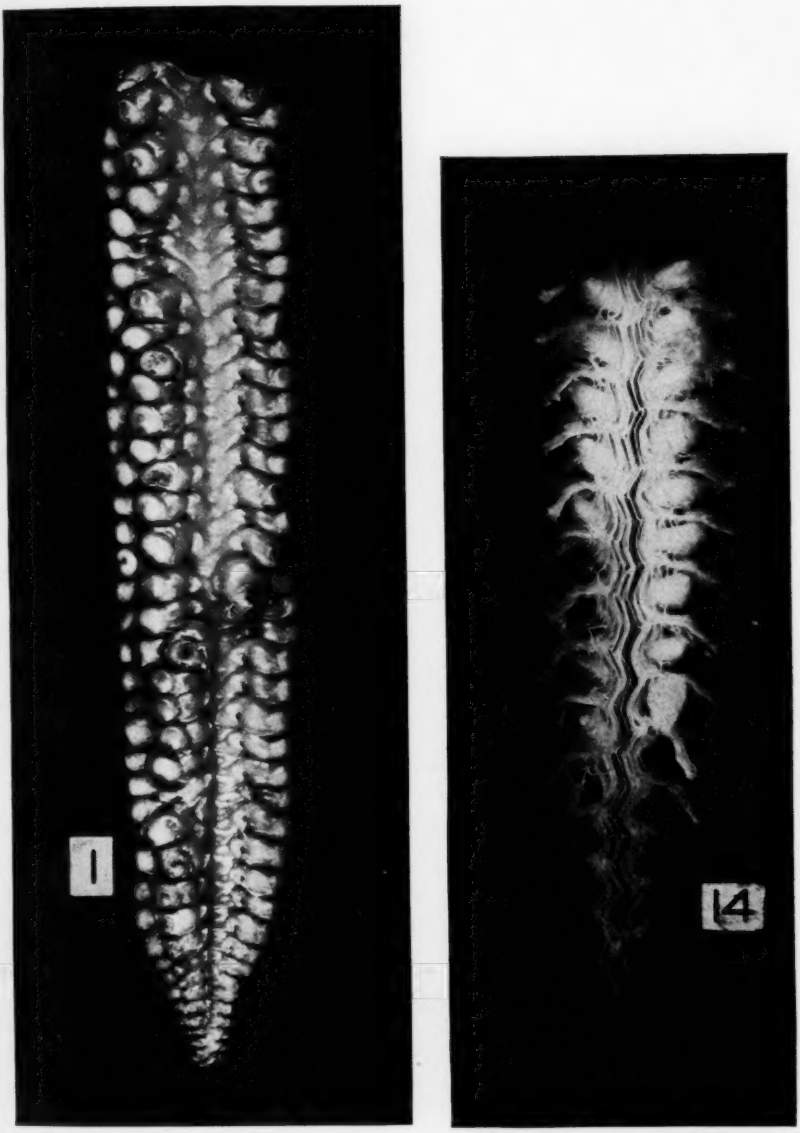
SUMMARY

The 4-rowed ear of corn shows a basic pattern of vascular tissue which resembles that of the 8-rowed ear. There exist pronounced inner and outer systems which probably differentiate at the base of the ear. The inner system furnishes the main vascular supply to the spikelets; the source of supply is more extensive circumferentially than in the 8-rowed ear. The outer system is associated with the supplies to the lower glumes. The presence of bundles of the inner and outer systems, which do not supply any organ, along the sides without spikelets indicates that a reduction has occurred.

Explanation of Plate

PLATE 36

Fig. 1. Side view of four-rowed ear of corn.
Fig. 14. Retted specimen of four-rowed ear.



LAUBENGAYER—ANATOMY OF FOUR-ROWED EAR

GENERAL FEATURES OF THE EPIDERMIS IN ZEA MAYS[1]

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I. TECHNIQUES FOR STUDYING THE EPIDERMIS OF CEREALS AND GRASSES

In the plant kingdom the epidermis reaches its highest degree of differentiation in the Gramineae. Therefore it displays in this group a rich choice of specific characters which can be used in the genetic study of cereals as well as in the general taxonomy of the family (Prat, 1932). To obtain valuable results in this field it is necessary to make a careful examination of the epidermis on all the parts of the plant, by using a wide range of techniques and enlargements.

A. *Direct examination.*—

First, all the leaves and internodes from the base to the summit of the culm, as well as the floral bracts, must be examined with a dissecting binocular. All the features of the epidermis should be noticed, and at this stage of the work a preliminary distribution map of the most conspicuous elements can be drawn. However, this direct examination is never sufficient, some categories of cells requiring higher magnifications than others; hence the necessity of making cross-sections and peels.

B. *Peels.*—

The shortest way to obtain preparations of the epidermis is to peel off portions with forceps. However, this is possible only in the most favorable cases, while the technique of scraping described below serves under almost all conditions.

C. *Scraping.*—

Place on a glass slide the part to be studied: leaf, internode, etc., *the epidermis which is to be examined being face down.* Scrape away carefully with a scalpel all the overlying tissues, removing everything except the epidermis in question. Then turn the piece of epidermis upside down for microscopic examination. This operation is, in general, easy and rapid with fresh tissues. Dry material as, for instance, herbarium specimens, may be put in a softening medium of equal parts of glycerin, alcohol and water, for two or three days before dissection.

D. *Staining.*—

The pieces of epidermis can be observed immediately under the microscope. For a more detailed study of the cell walls the best technique is a double staining, using methylene blue and ruthenium red: (1) Put the tissue in a solution of

[1]This article is a part of a wider investigation on epidermic characters of maize. Travel expenses were covered partly by the Missouri Botanical Garden, partly by a fellowship of the John Simon Guggenheim Foundation; material was provided by the experimental fields of California Institute of Technology, Missouri Botanical Garden, Pioneer Hi-Bred Corn Co., Harvard University, and Montreal Botanic Garden. I express my heartfelt thanks to Drs. George T. Moore, H. A. Moe, E. G. Anderson, Edgar Anderson, William L. Brown, P. C. Mangelsdorf, J. Rousseau, and H. Teuscher, for the help so kindly given.

methylene blue and alum for one-half minute; (2) wash it thoroughly; (3) place it in a watch glass in distilled water; then add a small quantity (less than a pinhead) of the powder of ruthenium red (solutions of this substance in water being unstable, it is necessary to prepare immediately at the time of use); let it remain for half an hour.

Cellulose cell walls will be colored a bright red, the intensity of color being chiefly in proportion to their content of pectic substances; sclerified cell walls will appear blue, suberous ones green. The progress of the ruthenium staining can be watched under the microscope until the desired intensity is reached. The preparation is then dehydrated rapidly in alcohol (70, 90, 100 per cent), put in xylol, and mounted in Canada balsam. Such slides can be kept indefinitely, though they decolorize slowly after some years. If ruthenium red, a rare and expensive substance, cannot be obtained, double staining by iodine green and alum carmine may be used successfully, though giving less brilliant colors.

E. *Observation.*—

The entire range of microscopic enlargements is useful for a study of the epidermis, from the lowest objectives for observing the general distribution of elements, up to immersion objectives for the tiniest cell details. All the resources of the condenser and of the diaphragm are needed to sharpen the contrasts between the elements and to accentuate their relief. For observing silica cells, hydrating mediums such as chloral lactophenol are useful in order to increase the difference in refraction indices between silica and neighboring tissues and to render those cells more conspicuous.

F. *Cross-sections.*—

Epidermic preparations obtained by peeling or scraping show the shape of the cells in vertical projection only. To recognize their other aspects it is necessary to examine also cross-sections of the whole organ, leaf or internode, both in transverse and longitudinal planes. These sections enable us also to observe the anatomical connections of epidermis cells with subjacent tissues. The best technique for staining them is again methylene blue and ruthenium red. After a careful microscopic examination of all epidermis preparations and cross-sections it is always necessary to examine again, in their living state, the entire organs of the plant with the dissecting binocular, in order to map the distribution of the elements precisely.

II. CATEGORIES OF ELEMENTS IN GRASS EPIDERMIS

Epidermis cells are regularly disposed in straight rows over almost the entire body surface of a grass. Some of them are elongated in the same direction as the organ on which they are borne (internode, leaf or bract), while others remain short; hence the classical distinction between "long cells" and "short cells." It is really better to distinguish "fundamental elements"—generally but not always elongated—and "differentiated elements."

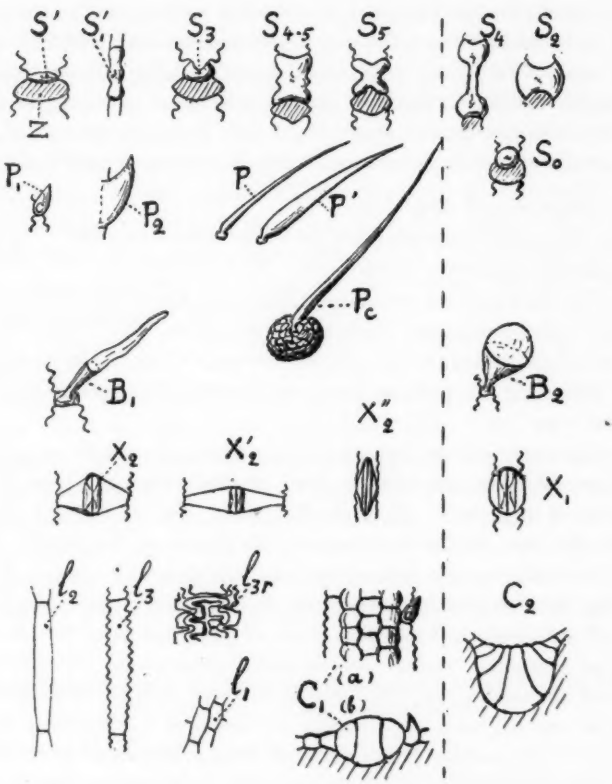

Fig. 1. Shapes of epidermic cells in grasses (structural characters). On the left of the broken vertical line, cells of *Zea Mays;* on the right, cells of other genera:

S, *silica cells:* S', S'_1, S_3, S_{4-5}, S_5, in *Zea;* S_4, in *Panicum* (shape widely distributed in panicoid tribes); S_2, in *Chloris* (shape general in chloridoid tribes); S_o, in *Hordeum* and festucoid tribes.

Z, *cork cells.*

Exodermic elements: P_1, small spicules; P_2, large spicules (profile); P, unicellular hair; P', swollen unicellular hair; P_c, cushion hair; B, bicellular hair; B_1, eu-panicoid shape; B_2, chloridoid shape.

X, *stomata:* X_2, lozengic shape present in *Zea*, with variants; X'_2, X''_2, X_1, ovoid shape (*Hordeum*).

l, *fundamental cells:* l_2, with straight walls; l_3, with undulated walls; l_{3r}, with thick and undulated walls; l_1, remaining short in transition zones.

C, *bulliform cells:* C_1, in *Zea* (a), vertical projection, (b) transverse section; C_2, in *Panicum* (transverse section).

It is worth noticing that only the first of these categories of cells is sensitive to auxins. At a given growth stage the length of a "long cell" in the meristematic base of an internode or of a leaf can be increased suddenly 200-fold in a lapse of several hours. During the same time the length of the adjacent "short cells" is only slightly modified. The body of these cells seems to escape the influence of growth hormones, probably on account of their precocious senescence; hence their shape is more constant and more interesting for displaying specific characters.

A. *Differentiated elements.*—

The differentiated elements fall into four great categories: (1) silica cells; (2) exodermic elements; (3) cork cells; (4) stomata.

1. The *silica cells* are precociously filled with a jelly of colloidal silica, which becomes a solid transparent block as the protoplasm dies. They may take the shape of halters, crosses, battle-axes, half-moons, etc., or be simply round or rod-shaped (fig. 1, *S*), these shapes being characteristic of sub-families and tribes of the Gramineae.

2. The *exodermic elements* include the differentiated cells or groups of cells which extend above the common level of the epidermis. Most of these are formed by a single cell: (1) *Unicellular hairs* (fig. 1, *P*); (2) Small or big *spicules* (P_1, P_2), which are present in all groups of the family. Others are formed by two or many cells, and they exist only in definite tribes: (3) *Bicellular hairs* (fig. 1, *B*), made up of two cells of different textures. The walls of the basal cell are strong and sclerified, those of the distal one, thin and cellulosic, giving an interesting example of unequal segregation of potentialities in the division of the mother cell; (4) *Cushion hairs* (fig. 1, *Pc*) consisting of big hairs formed by one cell but each arising in the middle of a hemispheric protuberance formed by a large number (20 or more) of small differentiated cells.

3. The *cork cells* (or suberous cells) (fig. 1, Z) do not by themselves exhibit characteristic shapes but are molded by neighboring elements. Their protoplasm dies early, being surrounded by impermeable walls of suberin. They offer an interesting case of cell polarity. When the mother cell of a differentiated cellular group divides, if a cork cell is produced it is always situated on the basal side of the group, i. e., toward the base of the organ. The other element, silicous or exodermic cell, is always apical.

4. The *stomata* (fig. 1, *X*) are formed by four cells, a special feature of the Gramineae, instead of two as is usual in other families. Their shape can be ovoid (X_1) or lozengic (X_2). Their distribution is interesting from the anatomical point of view on account of their connection with chlorenchyma, and from the ecological one. For example, in xerophytic species stomata are often absent on the outer face of the blade and localized on the inner face, being therefore enclosed in the leaf when it shrinks and rolls up into a tube during dry periods.

B. *Fundamental elements.*—

The fundamental cells always constitute the greatest part of the epidermic area. However, they are less interesting than the differentiated ones, their shapes being more uniform and exhibiting barely conspicuous specific characters. Their walls may be straight (fig. 1, l_2) or undulated in connection with small punctiform depressions in the outer wall (l_3). On strengthened regions these walls may become thick and deeply furrowed (l_{3r}). In certain species the outer wall may bear cuticular warts or hollow papillae. Cells of this category are generally much elongated. Their length may reach up to 300 times their width, but they may also, in certain areas, remain short, almost square (fig. 1, l), as in transition zones (nodes, sheath bases, blade bases). This is why the term of "long cells," usually applied to them, is a misnomer.

C. *Bulliform elements.*—

On the leaves of certain genera, chiefly on the inner face of the blade, regular stripes can be observed, consisting of "bulliform" cells. They are aquiferous, strongly turgescent cells, sometimes reaching a great volume by expanding perpendicular to the leaf surface (fig. 1, C_2). In vertical projection they are shorter than the neighboring fundamental cells (fig. 1, C_1a). They may be considered as a separate category, distinct from both fundamental and differentiated elements. By losing their water in dry air they function in the rolling of the leaf in some xerophytic species, hence the name "motor cells" which is sometimes applied to them.

III. DISTINCTIONS OF THE SUBFAMILIES OF GRASSES ACCORDING TO THEIR STRUCTURAL EPIDERMIC CHARACTERS

A. *Structural characters.*—

For an efficient utilization of epidermic features in taxonomy or genetics it is necessary, first, to recognize the respective values of all the characters which may be distinguished and to determine their order of subordination (Prat, 1933, 1936). Up to now we have referred only to the shapes of the epidermis cells and mentioned that they may differ from one group to another. In this way we find a first category—the *structural* characters. They are characters of the *first order*, i. e., they can be applied to distinguish the great subdivisions of the family: sub-families and tribes.

The first step in analyzing the epidermis of a Grass will be thus to determine *what shapes of cells are present*. In general, this is sufficient to reveal the subfamily, the tribe, sometimes the genus, and we can obtain this information on a tiny fragment of leaf some square millimeters in area; hence the importance of the method in certain practical researches, for instance, in tracing the origin of certain manufactured products.

B. *Subfamilies.*—

The subfamilies Bambusoideae and Panicoideae possess the most complicated shapes of silica cells (fig. 1, S_4, S_5) in the eu-panicoid tribes, (S_2) in the chloridoid ones. In the subfamily Festucoideae only the simplest types of silica cells (S, S_1) are present. In Bambusoideae and Panicoideae also there are bicellular hairs, threadlike (B_1) in the eu-panicoid tribes, and swollen (B_2) in the chloridoid. The cushion hairs (P_c), too, are correlated with the Panicoideae subfamily. The true Festucoideae never possess either bicellular or cushion hairs (Prat, 1936).

Thus we may distinguish the structural epidermic characters of the great subdivisions of the Grass family:

(1) Bambusoideae, primitive group including arborescent forms, with the most complex epidermis.

(2) Panicoideae, mostly a herbaceous group retaining complex shapes of epidermic cells but with a specialization appearing in two directions:

(a) *Eu-panicoid type* characterized by halter-shaped silica cells (S_4), threadlike bicellular hairs (B_1). Includes the tribes Paniceae, Andropogoneae, Maydeae.

(b) *Chloridoid type* characterized by silica cells molded in the shape of battle-axes with double edges (S_2) and by swollen bicellular hairs (B_2). Includes the tribes Chlorideae, Eragrosteae, Sporoboleae.

(3) *Festucoideae,* herbaceous subfamily showing a marked simplification of the epidermic cell shapes, absence of bicellular and cushion hairs, and only the simplest shapes of silica cells (S, S_1). This group includes the tribes Festuceae, Hordeae, Aveneae, Agrostideae.

These structural differences in the epidermis between the subfamilies are in perfect harmony with equally important anatomical and cytological differences which distinguish the same groups; for instance, the radial disposition of the chlorenchyma around the vascular bundles in the leaves of Panicoideae, but not in Festucoideae; the basic number of chromosomes, 7 in Festucoideae, 5 or 9 in Panicoideae (Hunter, 1934); the first green leaf of the seedling, narrow and vertical in Festucoideae, broad and extroverted in Panicoideae, etc. The geographic distributions, too, are different: Bambusoideae and most of the Panicoideae are localized in tropical regions; Festucoideae in temperate and cold countries.

The concordance between these diverse categories of characters—epidermic, anatomical, cytological, etc.—gives a practical basis for revising the systematics of the Gramineae in order to reach a more natural classification showing the real affinities of the genera (Prat, 1936), the present classifications still being artificial and inadequate in many parts.

IV. STRUCTURAL CHARACTERS OF THE EPIDERMIS OF *ZEA MAYS*

A. *Shapes of cells.*—

On the leaves of maize we found the following categories of epidermic cells (see fig. 1, left side):

(1)—silica cells of the types: S', S'_1, S_3, $S_{4\text{-}5}$, S_5.
(2)—small and big spicules: P_1, P_2.
(3)—thread-like bicellular hairs, B_1.
(4)—cushion hairs, P_c.
(5)—cork cells, Z.
(6)—quadricellular lozengic stomata, X_2.
(7)—fundamental cells, mostly with undulated walls, l_3, and also, on localized areas, the types l_{3r}, l_2 and l_1.
(8)—bulliform cells of the type C_1.

B. *Taxonomic position of Zea Mays.*—

This epidermic structure belongs strictly to the eu-panicoid type and agrees with the anatomical and morphological characters in placing the genus *Zea* in the subfamily Panicoideae, near the eu-panicoid tribes Andropogoneae and Paniceae. The recognized affinities of the Maydeae with the Andropogoneae are thus confirmed by the structural epidermic characters.

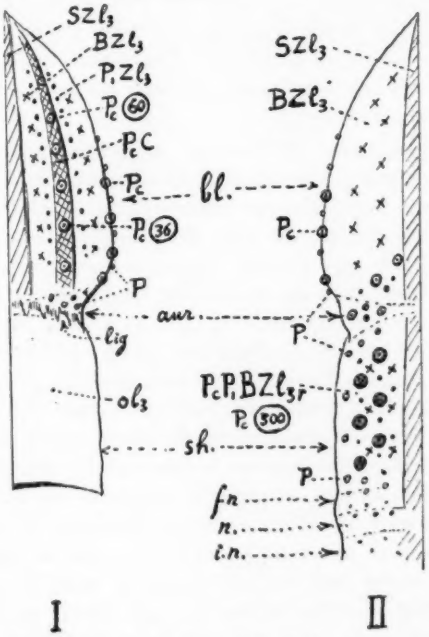

Fig. 2. Dermogram of the upper leaf, Mexican dent corn No. 1061 (distributive characters):

I, inner face of the leaf; II, outer face.

bl, blade; aur, auricular triangle; lig, ligula; sh, sheath; fn, false node; n, node; i.n., internode.

Letters representing the epidermic cells are the same as in fig. 1. Cushion hairs are figured by dots in circles (hatched when the cushion is colored red), ordinary hairs by circles, spicules (P_1) by dots, bicellular hairs (B) by crosses, bulliform stripes by cross-hatching, dense silica cells by hatching. Numbers in circles show the average density of cushion hairs per square centimeter.

V. DISTRIBUTIVE CHARACTERS; DERMOGRAMS OF CORN LEAVES

A. *Characters based on the distribution of epidermic cells.*—

The structural characters are not the only ones to consider in the epidermis of a Grass. The distribution of the different types of cells on all the organs of the plant (leaves, internodes, glumes, etc.) obeys precise rules and shows notable differences from one species to another, and within a species from one variety to another. The *distributive characters* thus constitute a second category of taxonomic importance. They are less fundamental but allow more delicate distinctions than the structural ones, as they provide a means of distinguishing smaller groups (species or varieties) instead of subfamilies and tribes. For this reason they are the most valuable for taxonomic or genetic work.

B. *Conception of dermograms.*—

The distributive characters can be shown in "dermograms," schematic maps figuring the position of the principal categories of epidermic cells. Figures 2 and 3 show examples of leaf dermograms for two varieties of Maize. The leaf represented must preferably be the upper one, just below the tassel, for this leaf displays to the utmost the specific characters. The leaves at the base of the culm are less differentiated, this fact being connected with the general law of histological gradation (Prat, 1934, 1945).

In figs. 2 and 3 only one-half of the leaf is represented, inner and outer face, and on this only one vein. The complete representation of all the veins with all their epidermic cover would give an infinitely complicated and useless diagram. For the need of simplification also, only the elements of interest for systematic comparisons are figured. For instance, stomata are not indicated on the scheme, their distributions being about the same in the varieties under comparison.

According to their size, spicules are figured by small or big dots (P_1 or P_2), unicellular hairs (P) by circles, bicellular hairs (B) by crosses, cushion hairs (P_c), by dots in circles. Regions where the differentiated elements are absent or consist only of stomata are left in white (ol); bulliform stripes (C) are represented by cross-hatching; regions with abundant silica cells (S) by hatching.

The precision of the dermogram can be increased by indicating the density of the most characteristic elements on different regions of the leaf. This density is easy to calculate by counting these elements in the field of a dissecting binocular for the biggest ones, such as cushion hairs, or in the field of a microscope for the smallest, such as bicellular hairs, and reducing to the unity of surface. On fig. 2 the numbers inscribed in circles indicate the local density of cushion hairs (P_c) per square centimeter.

C. *First example: Mexican Dent No. 1061.*—

The first example (fig. 2) is a small-seeded Mexican dent corn from El Capulin, bearing the number 1061 in the experimental cultures of Dr. E. G. Anderson, California Institute of Technology. The most striking feature of this

variety is the abundance of cushion hairs (P_c) on the entire outer face of the sheath (base of diagram II, fig. 2). Their density reaches here an average of 300 per square centimeter. On this area the cushion cells are colored a strong purple by an anthocyanin contained in their vacuole, and those cushions are conspicuous to the naked eye as small red dots. The hair itself is white, appearing under the microscope as a giant column with a constricted base, arising in the middle of the protuberance formed by the colored heap of dwarf cushion cells. The contrast between white hairs, purple cushions, and green surrounding tissues (chlorenchyma appearing through the uncolored flat epidermis) is striking when observed with the dissecting binocular, the more so as the cushion protuberances are strongly marked in this variety. The purple tint of the cushions appears only on the portions of sheaths exposed to the light.

On the outer face of the sheath the density of cushion hairs can reach up to 300 per square centimeter. We may notice also on the outer face small spicules (P_1), bicellular hairs (B), cork cells (Z) and, chiefly on the veins, silica cells (S). The fundamental cells present strongly undulated and thickened walls (l_{3r}). The inner face of the sheath (base of I, fig. 2) is covered by the simplest type of epidermis—only thin-walled fundamental cells (l_3) with few stomata.

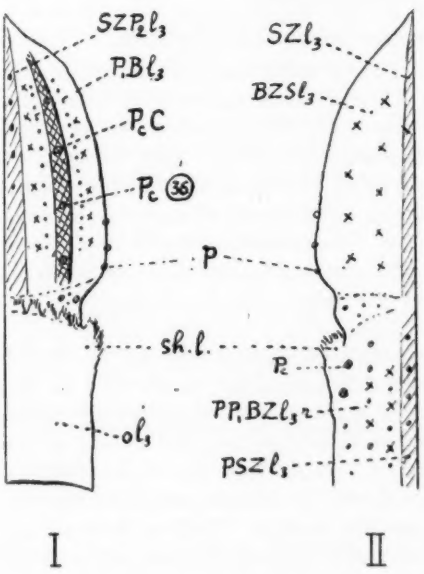

Fig. 3. Dermogram of the upper leaf, inbred yellow dent corn L317 (distributive characters):

Sh. l, sheath lobes; other conventions same as in fig. 2.

The inner face of the blade (summit of I, fig. 2) offers as its most striking feature conspicuous stripes of bulliform cells (C) located between the veins. On these stripes we observe from place to place big cushion hairs (P_c) analogous to those of the sheath, with the difference that their cushion is not colored purple though it is exposed to the light. On each side of a bulliform stripe is a dense row of small spicules (P_1). In addition, the inner face of the blade shows bicellular hairs (B_1), cork cells (Z), and chiefly on the ribs, silica cells (S). The fundamental cells (l_3) have undulated walls of medium thickness. In this variety the density of cushion hairs is lower on the inner face of the blade than on the outer face of the sheath; it can vary from 36 per square centimeter at the base of the blade up to 60 at the summit.

On the outer face of the blade (summit of II, fig. 2) we find no bulliform stripes, and only very rarely cushion hairs, localized at the base of the blade, mainly on the edges and on the auricular triangle. The exodermic elements are represented chiefly by bicellular hairs, spicules being scarce. The difference between the two faces of the blade can be recognized simply by feeling them with the finger tip, the inner face being minutely scabrous on account of its numerous small spicules (P_1), the outer face perfectly smooth to the touch. The bicellular hairs are too small and too soft to be perceptible.

D. *Second example: Inbred Yellow Dent No. L317.—*

Our second example is a yellow dent corn inbred, widely used in the United States corn belt, L317 (Cal. Tech. experimental field, Arcadia, summer 1948). The dermogram of this variety (fig. 3) differs from the preceding one chiefly by the outer face of the sheath (base of II). There the cushion hairs are very scarce and localized near the sheath lobes (these lobes are here much more developed than in the previous example). The cushion of these hairs is small, feebly protuberant, and not colored purple. The elements noticeable on the outer face of the sheath are ordinary hairs (P), spicules (P_1), bicellular hairs (B), cork and silica cells, the latter chiefly on the veins. The fundamental cells have thick, undulated walls (l_{3r}).

The inner face of the blade (summit of I, fig. 3) also shows some differences from the first example. Numerous big spicules (P_2) are borne on the principal ribs; on the bulliform stripes (C) cushion hairs are present, with an average density of 36 per square centimeter, but their cushion is very small compared to those of the first variety. On the outer face of the blade (summit of II, fig. 3) the cushion hairs are absent, but ordinary unicellular hairs can be noticed on the edges and on the auricular triangle. Bicellular hairs are present on the stripes between the veins, silica cells chiefly on the veins, and cork cells on both.

CONCLUSION

We have demonstrated for maize how it is possible to describe epidermic characters of cereals in order to use them in genetic and taxonomic studies.

1. When studying the epidermis of a cereal or a grass, the first step is to recognize its *structural characters*, i. e., the nature and the shape of its component cells. The shape of the silica cells (*S*), the presence and the shape of bicellular hairs (*B*), of cushion hairs (P_c), of bulliform cells (*C*), etc., must be specially investigated (see fig. 1). These structural characters give immediately the means to determine the general systematic position of the plant, i. e., the subfamily, tribe, to which it belongs. Each genus has a definite set of epidermis cells with well-defined shapes, as one of its fundamental characters. In all the species of a genus we find the same types of cells with exactly the same shapes, but they are differently distributed from one species to another.

2. The second stage of the study is therefore to determine how these categories of cells are distributed on the leaves and on the floral bracts. We thus obtain a second category of characters: the *distributive characters*, which may enable us to identify the species. This distribution of epidermic elements can be expressed in schematic maps or "*dermograms*" (fig. 2). The "*dermotype*" of a plant, the sum of its epidermic characters, will be thus expressed: (1) by a detailed drawing of each category of cells forming its epidermis (fig. 1), showing the structural characters and defining the general systematic position of the genus (subfamily, tribe); (2) by a *dermogram* (figs. 2 and 3) indicating the distribution of each type of cells on the outer and on the inner face of the leaf (the upper leaf being more characteristic, is preferably chosen), of the glume, lemma and palea. These dermograms show the distributive characters and give a means for typifying the species and varieties.

An interesting development in the genetic study of maize will be to identify the genes controlling the transmission of distributive epidermic characters, to analyze their linkage with other characters, and to find their positions in the chromosomes.

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COMPARATIVE HISTOLOGY OF THE FEMALE INFLORESCENCE OF *ZEA MAYS* L.[1]

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INTRODUCTION

While an interest in the corn cob has been shown by those who have attempted to explain the origin and nature of the ear, the increasing role which the cob is assuming today in industry, in archaeology, and in studies of the origin of maize makes it imperative that a careful comparative study of the cob be undertaken.

For many years corn cobs played no special role in the economy of corn production since approximately 90 per cent of the corn produced in the United States was used on the farms for feeding of livestock and most of it was fed as unshelled ears. The cobs remaining from ears that were shelled for poultry feed and the like were often used for fuel. However, with the advent of hybrid corn and large seed-processing plants, cobs have become a major by-product of a rapidly expanding agricultural industry and today ways and means are being sought for their utilization. Of the various uses suggested, one of the most promising is that of a filler in commercially processed feeds. There is some experimental evidence on the feeding value of ground cobs (Gerlaugh and Rogers, 1936), and further experiments are now under way. Other possibilities include its use in the production of furfural or as a substitute for peat-moss.

The corn cob plays an even more important role in the hybrid seed-corn industry. Since the grains of corn are produced on the cob, the physical characteristics of that structure affect the handling of the ear during processing. It is known, for instance, that certain corns are more difficult to shell than others, some shatter easily, and in some the grains are removed with difficulty. Some cobs are soft while others are hard and tough; certain cobs are very susceptible to ear-rotting fungi, while others are rarely attacked by these oganisms. Since these differences are of considerable importance to the practical corn-breeder it is necessary that the anatomical, histological, and chemical reasons for these differences be understood.

There is another reason why a comparative study of the maize cob is desirable. Both in North and South America archaeologists have excavated a large number of prehistoric sites and have found maize remains in many of these excavations. A few of the best finds have yielded remarkably well-preserved ears, without even a kernel missing, although the ear may have been stored for many centuries. However, at least 90 per cent of the material in archaeological collections is cobs. Since the mature cob is a hard and durable structure and not particularly attrac-

[1]Part of an investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfilment of the requirements for the degree of Doctor of Philosophy. The investigation was made possible by a special fellowship from the Pioneer Hi-Bred Corn Co., of Des Moines, Iowa.

tive to insects and rodents, it will remain relatively unchanged in trash heaps for long periods of time if kept dry, and many of the richest finds have been made in extremely dry areas. In more humid areas often the only plant material found consists of carbonized cobs and in such areas the cob assumes an even more important role than it does in dry areas. Through a study of the surface features of the prehistoric cobs certain facts about the corn can be arrived at, as, for example, the general shape and size of the ear. However, an entirely new set of characters which are present in the cob must be utilized if we are to make the greatest use of the vast quantities of material collected by the archaeologists. Before we can do this it is necessary to know which characters vary and the extent of their variation, and this can only be determined by making careful comparative studies of the anatomical and histological features of the cobs of various kinds of maize.

There is a fourth reason why a comparative study of the female inflorescences of maize is needed, and that is for a study of the origin of maize. One of the best approaches to a study of the phylogeny of most groups of plants is through comparison of the reproductive structures of that group. This is especially true in the Gramineae where the vegetative structures are of less importance than in certain other families. Today there is as great a mass of literature concerning the origin of maize as for any other crop plant, yet there has never been a thorough comparative study of the anatomical and histological features of its female inflorescence. Before a basic understanding of maize can be reached such a study must be made, not only of maize but also of its close relatives. The present investigation is a beginning along such lines and is an attempt to determine which are the variable features in the cob and the extent of their variability in different kinds of maize.

REVIEW OF LITERATURE

The origin and nature of the ear of *Zea Mays* L. have been subjects for speculation since Indian corn was first described and many hypotheses have been presented to account for it. Finan (1948) has made a critical survey of the descriptions of corn as found in the literature of the early Spanish explorations and in the great herbals. Because the ear of maize was a structure different from anything with which they were familiar the early herbalists devoted considerable attention to that structure and apparently the earliest-known European illustration of the plant is a detailed drawing of a mature ear.

Although the ear of maize has been known and discussed in literature over such a long period there is no part of the corn plant about which there is such a paucity of anatomical information as the mature cob. On the whole, the investigators who have written most about the ear, aside from those describing varieties of corn, have been primarily concerned with its origin and with the homologies between the ear and the tassel. The literature on the subject has become voluminous. The reader is referred to Mangelsdorf's (1945) recent paper in which he discusses (pp. 33–73) the major hypotheses concerning the origin of the ear.

The principal reason for the lack of information about the anatomy of the cob is that it is a difficult structure to study in its mature state. A cursory examination of the cross-section of an ordinary corn cob discloses that it consists of very different types of tissue. The center of the cob contains large soft-pith parenchyma cells surrounded by a layer of stone cells of varying thickness which are often compacted to form tissue as hard as that found in the shell of a hickory nut. Interspersed in these two such different tissues is the tough-branched network of the vascular system. Weatherwax (1935) summed up the difficulties of studying the cob when he said:

> "Long before maturity, however, the development of a tough schlerenchyma in the peripheral vascular region of the rachis makes it difficult to secure instructive sections even when the technique applicable to woody tissues is employed."

Not only is the cob hard and tough but it is composed of hard and soft tissues together, and if it is held firmly enough to make it possible to cut the hard parts the soft parts are apt to be crushed or broken.

While the anatomical features of the cob have not been well understood, the gross morphological features of the ear have been discussed by numerous investigators, especially in so far as those features could be used in describing corn varieties. John Lorain (1825) in his 'Nature and Reason Harmonized in the practice of Husbandry' described the varieties of corn grown in eastern United States in his time. It is evident from his book that he had a rather clear understanding not only of the basic types of corn grown in that region but even the effects brought about by the mixing of the different varieties. Bonafous, in 1836, monographed *Zea Mays*, describing the varieties of corn known to him, and in 1866 Enfield described a number of varieties. Sturtevant (1899) published the most comprehensive work on the classification of corn varieties that had appeared up to that time and which with only minor changes has been used until recently. Anderson and his collaborators (1942, 1946) have shown the need for a new classification of the races of corn which would incorporate all evidence available, especially the evidence from archaeology and genetics. Such a classification must be a goal toward which to work.

Most of the early authors, in their descriptions of corn, mention the cob and often remark about its strange character as, for example, Vasey (1884), when he wrote, "female spikes (originally by monstrous or teratological development?) are grown together into a spongy, continuous club-shaped body, the 'cob'." None of the early workers made comparative studies of the surface features of the cob. As Mangelsdorf (1945) has written, "though not easily interpreted [the ear] is not difficult to describe," and he describes it as "a spike upon whose thickened axis (the cob) naked grains (caryopses) are borne in longitudinal or somewhat spiral rows: eight, ten, twelve or more in number." Weatherwax (1935) gives a somewhat similar description, writing of it as "being made up of a cylindrical 'cob' around which the grains are arranged in eight or more parallel rows."

Collins (1919) is one of the first to have investigated the morphology of the ear in some detail. He brought in a new kind of evidence for this study by working with *Zea-Euchlaena* hybrids. He considered the primary morphological unit of the ear, as well as of the tassel, to be the organs borne in a single metamer of the rachis. In the pistillate inflorescence the members of this morphological unit occupy a single alveolus but since in the tassel the depression is too shallow to be termed an alveolus he proposed the word "alicole" to "designate the spikelet or spikelets, whether staminate or pistillate, that are borne in a single alveolus or at a single point on the rachis, considered as the axil or point of attachment of a reduced branch." According to Collins, there is evidence that the association of alicoles into pairs, "yoked alicoles," is more fundamental than their linear arrangement. In discussing dropping out of rows on the ear, Collins concluded that the dropped rows are on the opposite side of the ear and that this could occur if the two pediceled spikelets were dropped simultaneously from a pair of yoked alicoles. Weatherwax (1935) has shown that the rows of grains on the cob are paired because the spikelets are paired and has shown that the dropping of rows in the ear is due to one or more rows of paired spikelets having been discontinued and not to the dropping of one row from each of two or more rows of paired spikelets as Collins assumed.

Each of the paired spikelets consists of two florets, the lower floret usually aborting. However, in certain corns such as the sweet variety, Country Gentleman, both florets are often fertile, and Weatherwax (1935) showed that the crowding thus brought about by the extra grains breaks up the linear arrangement of rows and produces ears without distinct rowing.

Certain abnormalities of the ear have been described as, for instance, reversed kernels where the germ faces in a different direction from the normal. This condition was noted by Kellerman in 1891.

Studies of the early morphological development of the ear have been made by Fujita (1939) and Bonnett (1940). Fujita showed that in ears having odd number of pairs of rows (10, 14, 18, etc.) the rows tend to be twisted but that with even pairs of rows (8, 12, 16, 20) they tend to be straight. He is also the first to publish illustrations of thin cross-sections of the young developing ear. Bonnett (1940), by dissecting out young inflorescences in various stages, has presented a clear picture of the development of the superficial features of the ear. He has shown that the spikelet-forming branch initials divide into two unequal parts to form spikelet initials which then divide into two unequal parts to form the flower initials. In the ear the flower developing from the larger (upper) flower initial becomes fertile and the smaller (lower) one aborts in those corns in which there is a single fertile flower per spikelet. Subtending each spikelet-forming branch is a ridge which increases in size and forms the cupule in which the spikelets are borne.

Cutler (1946), one of the most recent authors who has studied the maize ear, stresses the point that the general opinion still persists that the origin of the ear must have been something unique and nearly miraculous. He discusses a number of grasses which do not ordinarily bear ear-like structures but on which they are found occasionally. These he shows are the result of fasciation. He does not imply, however, that these grasses are directly concerned in the evolution of maize but merely uses them as examples to show that the development of the ear and tassel may not be as unique a phenomenon as it is usually thought to be. He also describes an interesting arrangement of spikelets and alveoli found in a South American corn in which the alveoli, instead of having the linear arrangement as in other corns, are arranged like bricks in a wall.

Cutler also stresses the need for a careful comparative study of the ear. If a number of ear characters can be found which could be used in the classification of corns, he points out, it would be possible to include in the studies of the origin and distribution of the various races of maize the vast number of prehistoric ears which the archaeologists have collected.

METHODS

Any one who has handled mature corn cobs is aware that they may be very hard and tough and that some are almost impossible to break with the bare hand. Because of this excessive hardness it is necessary to devise a method whereby serial series of sections could be obtained thin enough for microscopic study. A modified celloidin method was developed which worked well with all materials used including prehistoric cobs from archaeological sites.

Ears of the desired varieties were shelled and the cob boiled for several hours in water to which had been added a few cc. of an aerosol solution. The solution is very effective in small quantities and was prepared by dissolving a small amount of American Cyanamid & Chemical Corporation "Aerosol OT," 100 per cent, in methyl alcohol and then adding an equal amount of water. The only precaution to be taken in its preparation is that the solid aerosol be dissolved in the alcohol before the water is added. The addition of a few cc. of this stock solution has the effect of lowering the surface tension of the water sufficiently so that dry cobs would wet immediately and sink, consequently reducing the time required for boiling. This thorough wetting of the cob made it possible to remove certain gummy substances which were not removed when they were boiled in water without the aerosol. After boiling, the cobs were washed in running tap water for several minutes and then cut into sections small enough to clamp into the microtome. Even after boiling it was often necessary to use a hammer and a heavy scalpel to cut the cob into sections. Small cobs were cut crosswise into sections approximately one inch long. Larger cobs were cut longitudinally into quarters or halves depending upon their size.

The material was dehydrated by running it through an alcohol series using 30, 70, 95 and 100 per cent strengths. Material was left in each of the various grades of alcohol 24 hours.

Two celloidin methods were tried, the regular one as outlined by Chamberlain (1932) and the Rapid Embedding Low Viscosity Nitrocellulose Method outlined by Koneff and Lyons (1937). Results obtained by either method were satisfactory, but since the latter is more simple and more rapid it was the one used in this investigation.

After dehydration the material was placed in a solution of equal parts of absolute alcohol and ethyl ether, where it was allowed to remain for one hour. It was then placed in small wide-mouthed bottles and a 10 per cent nitrocellulose solution added, after which the corks were securely wired in place and the bottles placed in a paraffin oven for 24 hours. The pressure built up in the bottles facilitates the infiltration of the nitrocellulose solution into the plant material. After removal from the oven the bottles were allowed to cool before opening. The 10 per cent nitrocellulose solution was then poured off and a 25 per cent solution added, after which the corks were secured and the bottles again placed in the oven. The following day a 50 per cent solution was added and the bottles placed in the paraffin oven as before. Upon cooling they were opened, and the material picked up by means of forceps and quickly plunged into chloroform where it was allowed to remain for 24 hours in order to harden the nitrocellulose. The chloroform was changed once during the 24 hours. Later the hardened blocks containing the embedded material were placed in 80 per cent alcohol where they were allowed to remain until sectioned.

All sectioning was done with a Bausch & Lomb sliding microtome. Because of the differences in the density of the tissues of the cob, microtome blades must be exceptionally sharp. All the blades used in this investigation were either sent to the factory or to a professional instrument grinder for sharpening. The number of sections obtained before resharpening of the blade is necessary varies with the hardness of the cob but usually from three to five cobs may be cut before the blade needs to be resharpened.

The nitrocellulose blocks were removed from the alcohol and excess embedding material was removed after which the blocks were clamped directly into the microtome. During the cutting the knife and block containing the embedded cob were kept flooded with 80 per cent alcohol, this being accomplished by "painting" them with a small camel's-hair brush dipped into the alcohol. Sections were prevented from curling by holding the brush on the surface of the block as they were cut. The individual sections were removed with the same brush and placed in the alcohol.

All staining was done with safranin and light green. Before staining, the nitrocellulose was removed from the plant material by placing the sections in equal parts of ether and absolute alcohol in small culture dishes for approximately 10 minutes. They were then washed in 95 per cent alcohol and placed in a dish containing water to which was added a few drops of a standard safranin solution (1. g. safranin, 100 cc. 50 per cent alcohol). Sufficient safranin was added to give the water a light pink color. The material was left in this stain over night

and the following day the sections taken out and the excess stain removed by placing them in 95 per cent alcohol to which had been added two drops of concentrated HCl per 100 cc. alcohol. The sections were destained until only a slight pink color remained in the parenchyma cells after which they were washed in 95 per cent alcohol and counterstained in light green dissolved in clove oil. Enough stain from the stock solution (1 g. light green, 100 cc. clove oil) was added to pure clove oil so that the sections would be sufficiently stained in one minute. They were then washed quickly in absolute alcohol, cleared in xylol, and mounted in Canada balsam.

Cobs from archaeological sites were handled in the same way except that after being boiled they were placed in hydrofluoric acid for a few days to dissolve any sand that might be present. The hydrofluoric acid was diluted to 50 per cent with water and placed in paraffin containers. The cobs were then placed in the acid and the containers placed under a hood. On removal from the acid the cobs were thoroughly washed in tap water, dehydrated, and handled like the other material.

TOPOGRAPHY OF THE MAIZE COB

It is difficult to interpret the morphology of an ordinary corn cob because its main features are obscured by the papery edges of the floral parts. Even under a dissecting microscope the cob (pl. 37, fig. 1) appears to be a mass of crowded wrinkled chaff of no apparent significance and with the mature cob it is difficult to remove enough of this tissue paper veil without at the same time destroying the underlying structures. Weatherwax (1935) prepared cobs for study by turning them in a lathe and removing all parts down to the hard rachis. Reeves (1946) successfully prepared cobs for study by treating them with sulphuric acid for twelve hours and then washing them in water.

One of the best places to study the surface of the cob is in the corn field. In young growing ears which have been fertilized but are not yet fully mature it is possible to snap off the spikelets with the fingers, leaving the rachis free from the parts that make the mature cob so difficult to study. A morning spent in examining young ears in a large collection will disclose the great variation to be found in the surface features of the cob. Corns possessing the gene (Vg) for vestigal glumes produce ears in which the glumes are so reduced that it is possible to study (pl. 37, fig. 2) the surface features of the rachis without any preparation. The outer glume, while present, is greatly reduced and the lemmas and paleae are almost completely suppressed, thus producing a cob with none of the chaff that makes ordinary cobs so difficult to study.

A typical ear of *Zea Mays* may be said to consist of a more or less elongated cylinder of hardened tissue (the cob) to which are attached pairs of fertile spikelets, usually borne in longitudinal or somewhat spiral rows. If the grains are removed, as well as the chaff and the glumes, to the point where the spikelets are attached to the rachis, it will be seen that the pairs of florets are attached near the lower outer edge of a depression or alveolus that extends into the thickened rachis.

Sturtevant (1899) called this depression a "cupule." Harshberger (1893) wrote, "spikelets . . . placed in a cucullate depression on a fleshy cob." Collins (1919) proposed the word "alicole" to designate "the spikelets, whether staminate or pistillate, that are borne in a single alveolus or at a single point on the rachis, considered as the axil or point of attachment of a reduced branch." Cutler (1946) recently has used alicole in a slightly different sense, thus: "each pair of grains arises from a pair of spikelets and comprises with the related parts of the cob the alicole." For brevity and clarity it is desirable to have a single word for the structure which has been called the "cucullate depression," "corneous cupule" or "alicole" by the different authors. Since alicole has been used in different ways it seems best to follow Sturtevant and call the structure a cupule. Throughout this discussion the word "cupule" will be used to designate the depression or alveolus on the cob near the base of which the paired spikelets are attached.

Weatherwax (1935) has shown that the pairs of spikelets on the ear not only maintain a linear relationship but also a lateral one, and he showed that the spikelets of one row were not opposite those of the adjacent row but alternate with them. He also showed that the dropping of rows in the ear is due to one or more rows of paired spikelets having been discontinued and not to the dropping of one row from each of two or more rows of spikelets as Collins (1919) had assumed. Cutler (1946) has described a race of maize from South America in which the cupules are arranged like bricks, each being covered with half a cupule from the right and half a cupule from the left, thus forming an ear with cross-spiralling of the rows. In other words, rows can be traced in a spiral around the ear in two directions. Thus a single grain will be part of a row that spirals to the left and also part of a row that spirals to the right.

Cupules are not unknown in other grasses. They are conspicuous in such genera as *Manisuris*, *Hackelochloa*, and *Tripsacum*. St. Augustine grass (*Stenotophyrum secundatum* (Walt.) O. Kuntze) bears rows of solitary fertile spikelets in cupules on a corky flattened rachis (Cutler, 1946). On close examination it will be seen that the cupules of different varieties of maize vary greatly in shape, in the depth to which they penetrate into the cob and in the development of tissue on the sides above the attachment of the spikelet pairs. In some varieties the cupule is shallow and almost saucer-shaped while in others it is much wider than it is high and penetrates deeply into the rachis. In many of the corn-belt varieties the cupule not only penetrates deeply into the rachis but tends to turn up at an angle. According to Bonnett (1940) the cupule develops from a ridge subtending the spikelet initials and is similar to the subtending leaf initials that appear in the differentiation of the inflorescence of barley, wheat, and oats. The development of the outer edge of the cupule was mentioned by Harshberger (1893) in describing *Zea Mays:* "spikelets paired in alveoli, strongly marginal and cupulate, the margins becoming hard and corneous." Arber (1934) has used the term "rachilla-flaps" for the non-vascularized outgrowths of the reproductive axis of certain grasses and has given as an example the outgrowths of the lip of an oblique cupule in

Cephalostachyum virgatum Kurz., an east Indian bamboo. Cutler (1948) has called the outgrowths of the margin of the cupule in maize, "rachis-flaps," and that term will be used in the following discussion. In certain races of maize the rachis-flaps are little developed and form only a slight ridge separating the cupules from the adjacent parts of the cob. In other races the rachis-flaps form very conspicuous outgrowths at the side of the cupule which may be several mm. in length, as, for example, the Mexican variety Cacahuazintle, which has rachis-flaps as much as 5 mm. in length and is flexible due to the presence of only a small amount of sclerenchyma. In varieties with highly sclerenchymatized cobs the rachis-flaps are usually hard and corneous.

Another variation apparent in cross-sections of the cob is the manner of insertion of the spikelet pairs on the cob axis. This is affected to a certain extent by the development of the rachis-flaps as well as by the depth of the cupule. Cross-sections of certain varieties show the spikelets attached directly to a more or less cylindrical rachis, while other corns, especially United States corn-belt varieties, have the spikelets attached at the bottom of a cup-like depression. A closer inspection will disclose that this difference is due to the fact that in the first case the cupule is very shallow and the rachis-flaps only slightly developed while in most corn-belt varieties the cupule is well developed and extends a considerable distance into the rachis and the rachis-flaps tend to be well developed.

The length of the pedicels of the spikelets varies in different races of maize and has been mentioned by various investigators (Mangelsdorf & Cameron, 1942; Cutler, 1946). In some races of corn such as the northern flints as defined by Brown and Anderson (1947) the spikelets are attached by a broad base to the lower margin of the cupule so that there is no definite line of separation between the glumes and the cob. In certain varieties from South America and from Asia the spikelets are distinctly pedicellate, and the pedicels may be up to 2 mm. in length.

INTERNAL ANATOMY

Just as the cob varies in its surface features, so it also varies in its internal features. Cross-sections show great variation in the proportion of sclerenchyma and pith. Four distinct zones may be differentiated in the cross-section of an average corn-belt cob as follows: (1) Immediately inside of the epidermis there is a more or less solid ring of thick-walled lignified cells inside of which there is, (2) a cylinder of pith composed of large thin-walled parenchyma cells. Lying embedded in these two zones is (3) the vascular network which, at least in certain races of maize, consists of two rather distinct tubes of vascular bundles, one inside of the other (Reeves, 1946; Laubengayer, 1946). Their location relative to the other zones will be discussed more fully later. (4) The fourth zone consists of branched parenchyma cells which surround the vascular bundles as they leave the inner vascular tube and extend out into the spikelets.

Sclerenchyma.—

The texture of the cob, whether fibrous and flexible or lignified, hard and stiff, depends to a large extent upon the relative amount of sclerenchyma contained. Most North American corn-belt varieties have a hard tough cob. The cross-sections of such types show a well-defined sclerenchyma zone forming a nearly solid tube between the epidermis and the pith. It is within this mass of thick-walled cells that the cupules are located and in such varieties the rachis-flaps, as well as the outer glumes of the spikelets, tend to be heavily sclerenchymatized. There are other races of maize which tend to have rather soft cobs, as, for example,

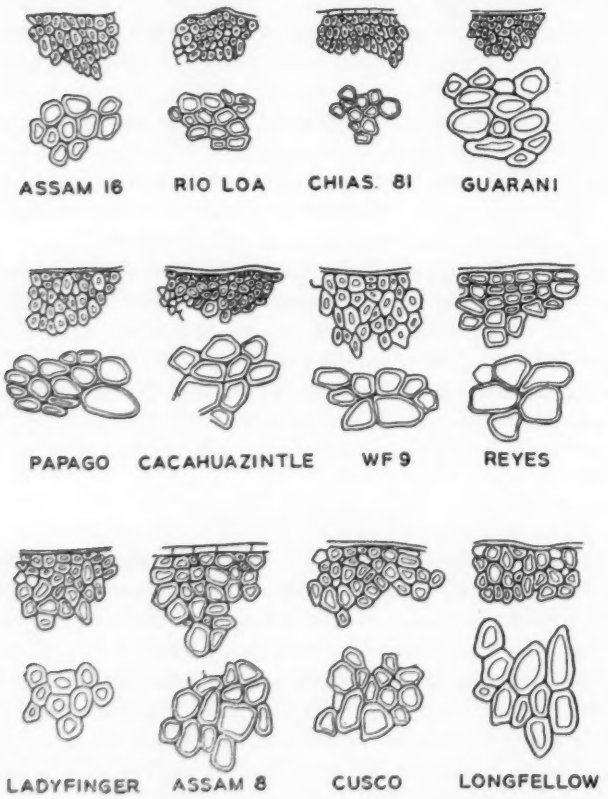

Fig. 1. Camera-lucida drawing of sclerenchyma. In each case upper drawing shows cells from immediately under the epidermis, lower drawing shows them half way between the epidermis and the pith.

certain South American varieties which are so delicately constructed that one can push the grains into the cob with the finger (Mangelsdorf & Cameron, 1942). In such cobs the sclerenchyma is present only as a relatively thin layer surrounding the cupules, and the rachis-flaps tend to be sclerenchymatized only on their inner face, while the glumes (Cutler, 1946) may even be delicate membranes.

The sclerenchyma tissue itself varies considerably in different corns. The cells may be relatively small and densely packed or larger and rather loosely packed. The distinction between sclerenchyma cells and pith cells, while abrupt and distinct in most corns, may show a rather wide area of transitional tissue where the cells become progressively larger and less thick-walled as they approach the central pith area.

Within any one cob the shape of the sclerenchyma cells varies greatly depending on their location. Both sclereids and fibers are found. According to Eames and MacDaniels (1947), the classification of sclerenchyma into sclereids and fibers has no morphological significance and is only used for convenience in description. In the sclerenchyma of the cob there is every gradation from typical fiber cells many times as long as wide to isodiametric sclereids. They may be smooth in outline or variously lobed. One unusual type of cell present in the cob is the branched parenchyma cell discussed in detail below. In some areas these cells become thick-walled and lignified and can thus be termed "astrosclereids." The size of the sclerenchyma cells and the amount of thickening of the cell wall vary in different races of corn as shown in fig. 1. The pits are small and the pit canals are usually unbranched. This character, as shown by Eames and MacDaniels (1947), is of little value in classification, being dependent to a large extent upon the thickness of the cell wall.

Pith.—

Nearly all corn cobs possess a central cylinder of pith. Prehistoric cobs often appear to be hollow, due to the decomposition of the soft parenchymatous tissue that originally filled the center of the cob. In general, the pith is rather uniform in the different races of maize, the cells being nearly isodiametric and thin-walled. However, the cell size varies in different corns, some varieties having more and larger intercellular spaces than others. As has already been mentioned, there is sometimes a rather wide area of transitional cells between the thick-walled sclerenchyma and the thin-walled parenchyma. There is also an area of transitional cells between the regular parenchyma pith cells and the highly branched parenchyma cells which form the sheath around the vascular bundles as they enter the spikelets. In the cobs of certain corns there may be a ring of cells in the pith which are colored and slightly thicker-walled than the surrounding pith cells. These are the so-called "pith-rings" of the corn-breeders. Pith-rings are commonly found in North American corns and have also been found in early prehistoric corn from Arica, Chile.

Vascular System.—

It has been difficult to obtain a complete understanding of the vascular system of the corn plant because of the difficulty in making preparations of certain portions, especially of the node and ear. Evans (1928), in discussing the vascularization of the node of *Zea Mays*, wrote:

> "Imbedding of tissue from the node and then sectioning has been found inadequate in the study of the node, since the branching of the vascular bundle is so intricate and the branches so tortuous as to defy solution even in the best prepared serial sections."

He developed a method of staining the vascular bundles in the stalk and then subjecting the sections to retting action by bacteria. After removal of the decomposed parenchymatous cells he was able to study the vascular network of the node of the corn stalk. He concluded that single vascular bundles seldom pass through more than two or three nodes without branching and further that "so complicated does this branching become that it is impossible of tracing even when no other tissues are present to complicate the situation."

Reeves (1946), in studying the vascular system of the mature ear, also used a retting process involving cellulose-digesting microorganisms. He was able to separate the vascular system from the other parts of the cob. Laubengayer (1946), using much the same technique, studied the vascularization of the cob of a northern flint. He showed that the vascular arrangement of the shank was essentially that of the main stem. However, in the transitional region from shank to ear the bundle system reorganized itself into two distinct systems, one inside of the other. The inner vascular system, with its larger bundles, supplies the spikelets, while the outer tube of smaller and more-branched bundles supplies the other parts of the cob. This arrangement of the bundles as shown by Laubengayer differs from that described by Weatherwax (1935), who says that the vascular bundles of the cob are distributed in approximately the same manner as those of the stem except for a tendency toward peripheral arrangement. Laubengayer's interpretation would seem to hold true for the majority of the cobs examined in this investigation. There are, however, varieties in which the vascular bundles are more or less evenly distributed throughout the pith of the cob, as, for example, in the inbred line Illinois R4, and in such cases it would appear that the inner vascular system would then form more of a cylinder of vascular bundles rather than the hollow tube of bundles as demonstrated by Laubengayer for the northern flints. That these two vascular systems are not entirely free from one another has been shown by Cutler (verbal communication). He was able to find small branches which connect the two systems at the nodes and he also found that a bundle that is originally a member of the inner system may later become a member of the outer system.

The location of the two fibrovascular systems relative to that of the sclerenchyma tissue varies greatly. In general, in cobs with large amounts of sclerenchyma, as, for example, those of the North American corn-belt varieties, the outer vascular system lies embedded within the sclerotic tissue. The inner cylinder, the

one supplying the spikelets, tends to lie along the line separating the sclerenchyma from the pith. Some bundles, however, may be located in the pith a slight distance from the sclerenchyma layer, in which case there may be a lobe of sclerenchyma tissue extending into the pith and surrounding the bundles with a sheath of sclerenchyma tissue a few cells thick. Since all the bundles are surrounded by a sclerenchymatous bundle-sheath it would appear in some cases that this lobe of sclerenchyma tissue does not actually surround the bundle itself because the layer of sclerenchyma cells around the bundle is no thicker than that found in the regular bundle-sheath. In some varieties such as inbred line Illinois R4, a considerable number of vascular bundles will be found distributed throughout the pith zone. In most corns some vascular bundles of the inner system will be found embedded within the sclerenchyma.

In races of corn which have cobs less sclerenchymatized than the rather extreme corn-belt varieties, the outer vascular tube tends to occupy the parenchymatous areas lying between the masses of sclerotic cells.

The vascular bundle of the corn plant has long been used in elementary classes as a typical example of a vascular strand, and since so many writers (Hayward, 1939, Holman & Robbins, 1939) have described the cells of which it is composed it need not be discussed here. No essential difference is found in the structure of the bundles of the two systems except that of size.

Branched Parenchyma.—

One of the most unusual types of tissue found in the maize cob is the branched parenchyma cells which are located between the sclerotic tissue and the vascular strands near the base of the spikelet and extending some distance into it. According to Eames (personal communication) the presence of these cells in corn is surprising, as is also their location. The inner edge of this zone lies near the inner vascular system, and cells transitional between pith parenchyma and the branched parenchyma may be found. The branched parenchyma cells tend to be considerably smaller than the pith parenchyma cells and are usually somewhat elongate with numerous branches, although they may be almost stellate in shape. The tips of the branches often are enlarged and may be nearly twice the diameter of the rest of the branch. The cell walls of these cells are usually thin but near the sclerotic zone some of the cells may be lignified, and in such cases they could be classified as "astrosclereids."

DISCUSSION

Of the anatomical and histological characters of the cob which are capable of exact measurement three characters vary greatly between the different varieties, namely, (1) The rachis-flaps, (2) the length and shape of the pedicels, and (3) the amount and distribution of the sclerenchyma.

(1) *Rachis-flaps.*—One of the most conspicuous differences in the cross-sections of the various varieties of maize is found in the rachis-flaps which vary in

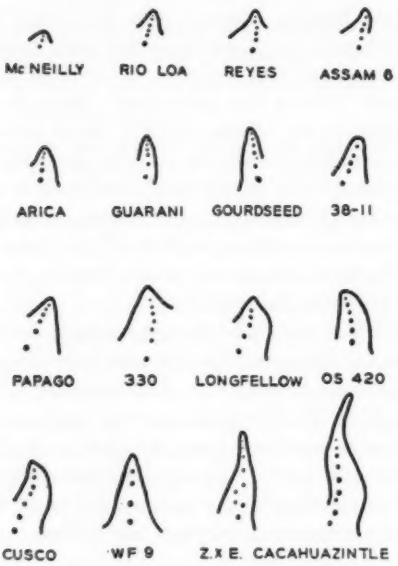

Fig. 2. Outline drawings of cross-sections of rachis-flaps made at the point of greatest development. Black dots are vascular bundles.

both size and shape. As defined in this paper, rachis-flaps are the outgrowths from the side of the cupule. They vary from a slight ridge separating the cupule from the adjacent parts of the cob (as, for example, in Ladyfinger popcorn) to the extremely long flexible appendages found in the Mexican variety, Cacahuazintle. To obtain an exact measure of the rachis-flaps, their outline was traced on paper from prepared cross-sections by means of a Bausch & Lomb microslide projector. The extent of variation of this character is shown in fig. 2. It is evident that Ladyfinger, Rio Loa, Reyes, Bolivia and Assam #6 and the prehistoric Arica varieties have the least developed rachis-flaps and that the most strongly developed ones are found in North American and Mexican varieties—inbred line WF 9, *Zea-Euchlaena* back-crossed to *Zea*, and Cacahuazintle.

From the varieties so far studied it would appear that the presence of well-developed rachis-flaps is due to *Tripsacum* contamination. The evidence for this, while not conclusive, is suggestive. Except for Cacahuazintle, the greatest development of rachis-flaps is found in the *Zea-Euchlaena* cross and all other varieties possessing well-developed rachis-flaps also show other tripsacoid characters. Cacahuazintle is a high-altitude Mexican variety. From the criteria advanced by Mangelsdorf and Reeves (1939) Cacahuazintle would in general be non-tripsacoid.

Fig. 3. Camera-lucida drawings of longitudinal sections of pedicels and glume bases.

The development of the excessively long rachis-flaps might be explained as due to an extreme recombination of characters derived from *Zea* and from *Tripsacum*.

(2) *Pedicel Length.*—As has already been mentioned by several authors (Mangelsdorf, 1945; Cutler, 1946) the length of the pedicel varies in different varieties of maize. They have described the long pedicels found in certain South American varieties. The pedicel not only varies in length but also in width and in shape; some of the South American and Oriental varieties have long and thin pedicels while other varieties may have equally long but relatively much thicker ones. In order to obtain a measure of this character slides were projected as before and the outline of the pedicel traced on paper. Since length and thickness are both important, the length of the pedicel was divided by the width in order to arrive at a significant measure of the relative length and thickness of the structure. Results are shown in fig. 3. The longest pedicel found in any variety studied was in Assam #8 (see pl. 38, fig. 6). In this variety the pedicels are rather thin and may be as much as 2 mm. in length, equal to any reported by Cutler for Andean corn. The fact that the pedicels are borne in a shallow cupule makes their length more noticeable than if the cupule were deep. In the commercial four-way hybrid, Pioneer 330, which has rather extremely long pedicels for North American corn,

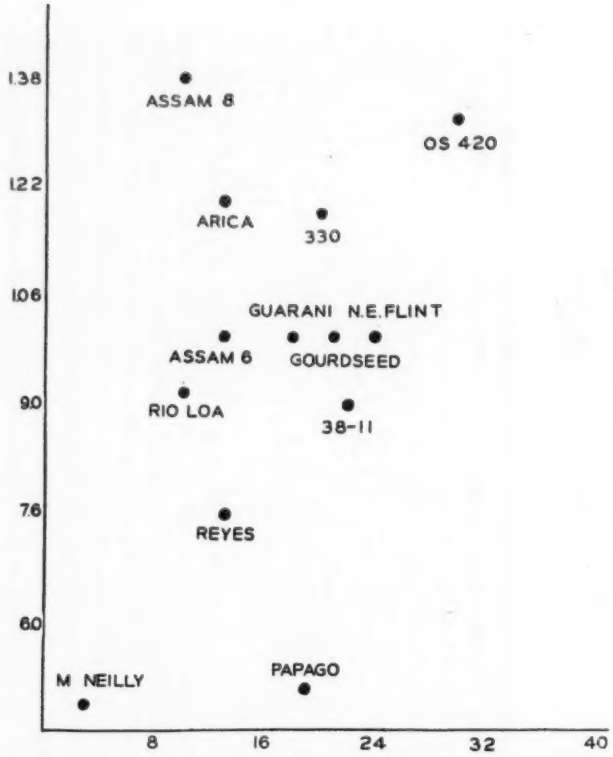

Diagram I. Scatter diagram showing relationship between pedicel length and length of rachis-flaps: horizontal axis, length of rachis-flap in mm.; vertical axis, pedicel length in per cent of pedicel width. Note that "McNeilly" in diagram is referred to as "Ladyfinger" in the text.

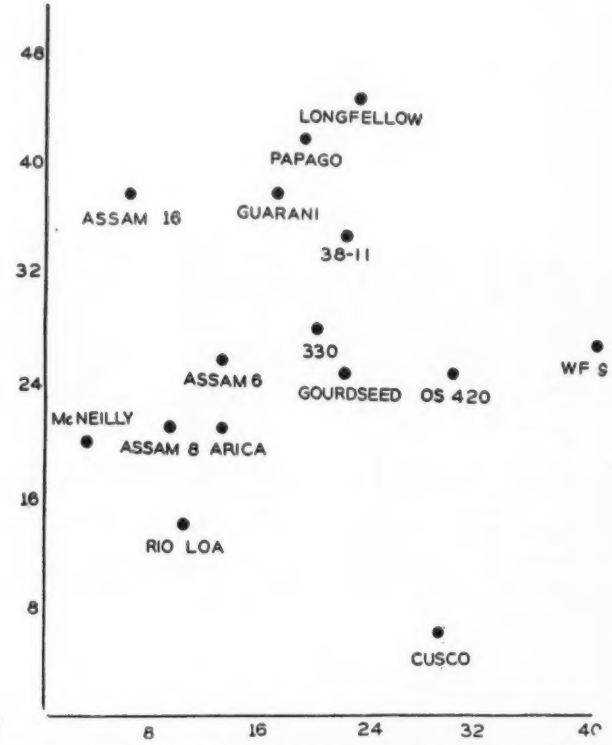

Diagram II. Scatter diagram showing relationship between rachis-flap length and per cent of sclerenchymatization of the cob: horizontal axis, rachis-flap length in mm.; vertical axis, per cent of sclerenchymatization of cob.

they are less conspicuous than in the South American and Oriental varieties since they are set in a deep cupule. The pedicels in Pioneer 330 are also broader in relation to their length than those in Assam #8. Among those varieties having short and thick pedicels are Gourdseed, Longfellow and New England Flint. According to Cutler (1946) one of the most obvious effects of tripsacoid influence is the shortening of the pedicels and the sinking of the whole spikelet into the cupules.

(3) *Sclerenchyma.*—Stained sections show great intervarietal differences in the amount of sclerenchyma. This is noticeable from stained slides even without the use of a microscope. Since the distribution of the sclerenchyma, as well as the amount, varies from variety to variety, it was necessary to measure the differences in the same relative place on all the cobs. After some preliminary trials it was decided to measure the thickness of the sclerenchyma at the point where the cupule extended the greatest distance into the cob. Slides of cross-sections were projected and the outline of the cupule traced showing the extent of the sclerenchyma. This was then divided by the radius of the cob at that point. This was called the degree of sclerenchymatization of the cob. It varies in the different varieties from 5 to nearly 50 per cent of the cob at the point measured. Since this character varies considerably within a single cob all sections used for comparative study were from near the center of the cob.

The least sclerenchymatized variety studied is Chiapas #81 (Rockefeller Foundation collection number), a flexible-cobbed variety. Here the sclerenchyma forms only a thin layer surrounding the cupule. Other varieties possessing small amounts of sclerenchyma are Rio Loa, Cusco, Assam #8, Arica and Ladyfinger popcorn. Among the most highly sclerenchymatized varieties are Longfellow, Papago, Guarani and inbred line 38-11. According to Mangelsdorf and Cameron (1942) *Tripsacum* contamination tends to impart a coriaceous quality to all parts of the cob. Of the highly sclerenchymatized varieties studied all possess other characters which would indicate that the variety is highly tripsacoid.

SUMMARY

1. The anatomy of the female inflorescence of *Zea Mays* (the corn cob) is of importance in corn-breeding, in studies of archaeological maize, and in considering the phylogeny of maize and its relatives.

2. Thin sections of mature corn cobs, both of recent and archaeological material, were prepared by a modified celloidin technique which is described in detail.

3. The topography of the mature cob is described. The main features of the cob surface are: The paired spikelets, (b) the associated cupule (or alveolus) and (c) the outgrowths from the side of the cupule, the rachis-flaps. The pedicels of the spikelets vary greatly in different varieties of maize, both in length and in shape. Certain varieties have pedicels as much as 2 mm. in length. Cupules vary from shallow depressions on the rachis, to deep cavities

penetrating a considerable distance into the cob. The rachis-flaps vary from slight ridges separating the cupule from the adjacent parts of the cob to long flexible appendages as much as 5 mm. long.

4. In cross-sections of mature cobs four distinct types of tissue are found, exclusive of the epidermis. They are: (a) A sclerenchyma zone, (b) a cylinder of pith, (c) the highly branched vascular system which consists (at least in certain varieties) of two rather distinct cylinders of vascular elements one inside of the other. The inner system supplies the spikelets and the outer system supplies the other parts of the cob, and (d) branched parenchyma cells which surround the vascular strands as they leave the inner vascular cylinder.

Great variation exists in the amount and location of the sclerenchyma in the cob, and varieties with "soft" cobs are shown to contain smaller amounts of sclerenchyma than "hard" cobs. The location of the inner vascular system varies but tends to occupy the area between the pith and the sclerenchyma. The outer vascular system is embedded within the sclerenchyma in highly sclerenchymatized varieties and the area between the masses of sclerenchyma in varieties which are only slightly sclerenchymatized. Nearly all cobs possess a pith center. The size of the parenchyma cells and the number of intercellular spaces vary in different varieties.

5. Three characters were found in the cob which varied greatly between the different varieties of maize, and methods were devised to measure these differences. *Rachis-flaps:* The least-developed rachis-flaps are found in Ladyfinger popcorn, Rio Loa, Reyes, Assam #6 and the prehistoric Arica, Chile, corn. The greatest development of rachis-flaps are in Mexican and North American varieties, Gourdseed, inbred line 38-11, Papago, Longfellow, OS-420, WF-9 and Cacahuazintle. *Pedicel length:* Pedicels vary from short and thick to long and thin. Assam #8, Pioneer 330, Arica, Assam #6 and Rio Loa have relatively longer and thinner pedicels than the varieties, Longfellow, inbred line 38-11, Reyes, and Gourdseed. *Sclerenchyma:* The amount of sclerenchyma in the different varieties of corn varied from 5 to 46 per cent of the radius of the cob at the point measured. The least sclerenchymatized varieties were Cusco, Rio Loa, Assam #8, Arica and Ladyfinger popcorn. The most highly sclerenchymatized varieties were Longfellow, Papago, Assam #16, Guarani and inbred line 38-11.

SOURCE OF MAIZE VARIETIES STUDIED

ARICA—Junius Bird, Am. Mus. of Nat. Hist.—from excavations at Arica, Chile.
ASSAM #6—Naga Hill Tribes, Assam, India.
ASSAM #8—Naga Hill Tribes, Assam, India.
ASSAM #16—Naga Hill Tribes, Assam, India.
CACAHUAZINTLE—Rockefeller Foundation Collection, Mexico, D. F.
CHIAPAS #81—Rockefeller Foundation Collection, Mexico, D.F.
CUSCO—Lehman Collection, Cusco, Peru.
GOURDSEED—Grapevine, Texas.
ILLINOIS R4—Pioneer Hi-Bred Corn Co., Johnston, Iowa.

LADYFINGER—McNeilly Seed Co.
MCNEILLY—see LADYFINGER.
PAPAGO—L. W. Lenz, Papago Indian Reservation, Sells, Arizona.
PIONEER 330—Pioneer Hi-Bred Corn Co., Johnston, Iowa.
REYES—H. C. Cutler, Reyes, Bolivia.
RIO LOA—Carl and Jonathan Sauer, Chiu Chiu, Chile.
VESTIGIAL GLUME (*Vg*)—DeKalb Hybrid Seed Corn Co., DeKalb, Ill.

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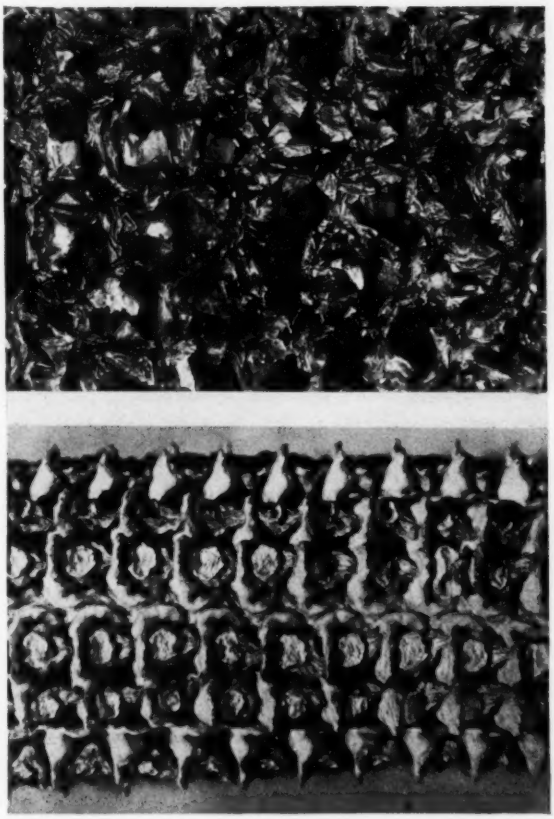
Explanation of Plate

PLATE 37

Fig. 1. Surface view of an ordinary cob showing remaining parts of spikelets. Scarious edges of floral parts conceal nearly all of the surface detail of the rachis. The white broken ends of the pedicels can be seen in a few places.

Fig. 2. Surface view of a cob from plant homozygous for vestigial glume (Vg). Reduction of glumes and lemmas reveals the following surface details: (a) paired spikelets, (b) rachis-flaps clearly seen at center of photograph, (c) alternate arrangement of pairs of spikelets on adjacent pairs of rows, (d) cupule extending into rachis behind the broken ends of the pedicel.



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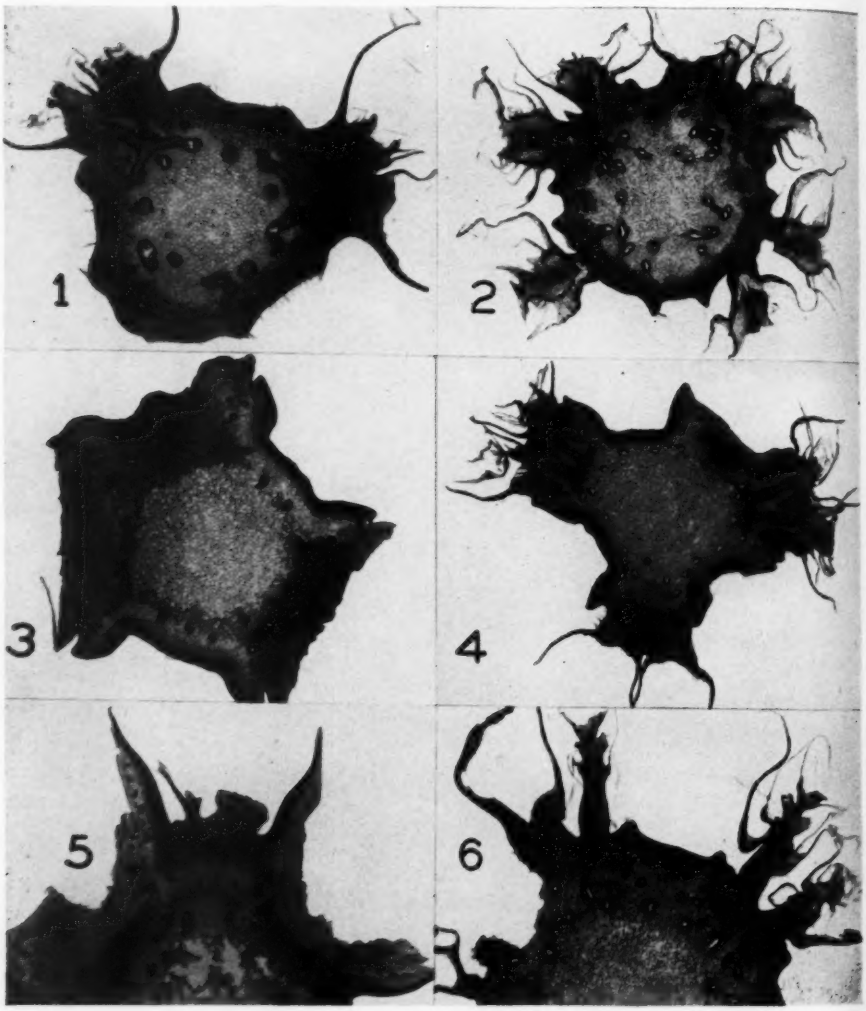
LENZ—HISTOLOGY OF THE CORN COB



LENZ—HISTOLOGY OF THE CORN COB

Explanation of Plate

PLATE 38

Photomicrographs of cross-sections of corn cobs: (1) Ladyfinger, (2) Reyes, (3) Chiapas #81 (flexible cob), (4) Arica, Chile (prehistoric), (5) Cacahuazintle, (6) Assam, India, #8.

Explanation of Plate

PLATE 39

Camera-lucida drawings of a serial series of cross-sections of the cob of a United States commercial "hybrid" variety (Pioneer 330). Solid black, dense sclerenchyma; stippled, ordinary sclerenchyma; white, parenchyma.

Fig. 1. Showing pair of spikelets set deep in the rachis.

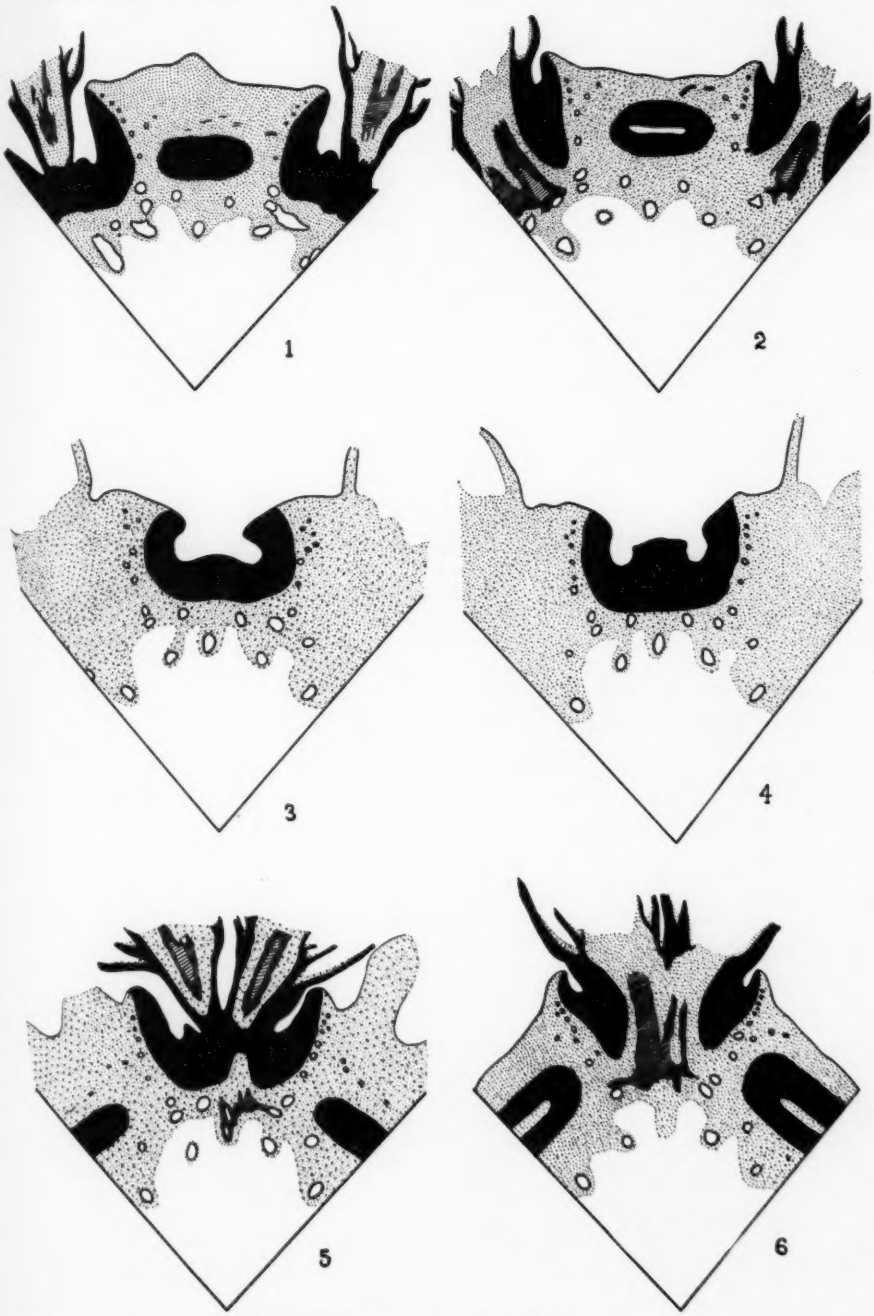
Fig. 2. Beginning of next cupule above and between the spikelets shown in fig. 1; first seen as an area of less dense sclerenchyma inside the center of dense sclerenchyma, later an opening appears in this mass of sclerenchyma.

Fig. 3. Opening which first appears in fig. 2 increases in size outward until it reaches the surface and opens out to form the cupule.

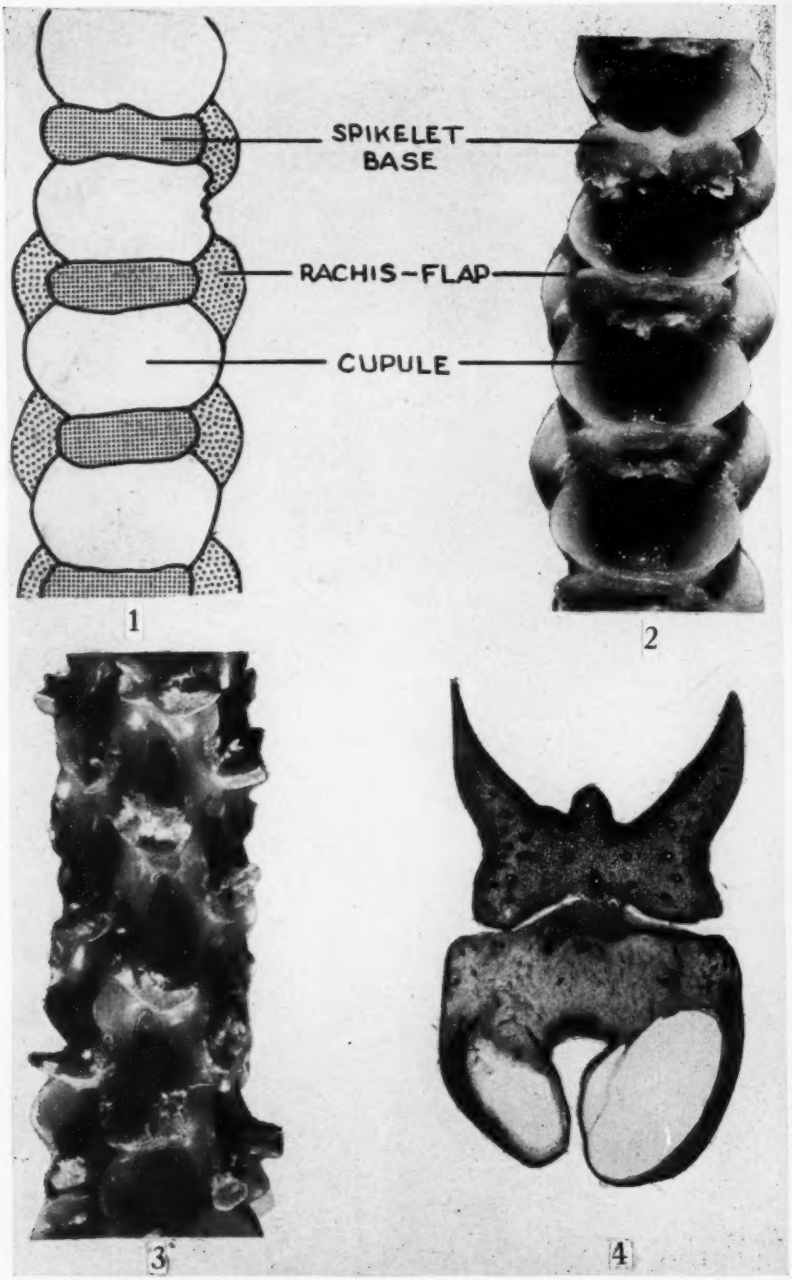
Fig. 4. Cupule with pedicel of spikelet pair rising out of it.

Fig. 5. Cupule with longitudinal section of pair of spikelets.

Fig. 6. Areas of dense sclerenchyma at either side of spikelets show the beginning of the cupules which will appear immediately above the spikelets shown in fig. 1.



LENZ—HISTOLOGY OF THE CORN COB



LENZ—HISTOLOGY OF THE CORN COB

Explanation of Plate

PLATE 40

Figs. 1 and 2. Photograph and tracing of photograph of immature 4-rowed cob from F_1 plant of *Zea* × *Euchlaena* with spikelets dissected out.

Fig. 3. Six-rowed cob from F_1 plant of *Zea* × *Euchlaena*. This cob produced only a single spikelet on each cupule.

Fig. 4. Cross-section of the 4-rowed cob illustrated in fig. 2. Note size and shape of rachis-flap.

Explanation of Plate

PLATE 41

Serial series of longitudinal sections of Chiapas #81 (flexible cob), a variety with little sclerenchyma tissue.

Fig. 1. In a few places the vascular strands of the inner system can be seen. The small bundles of the section belong to the outer vascular system.

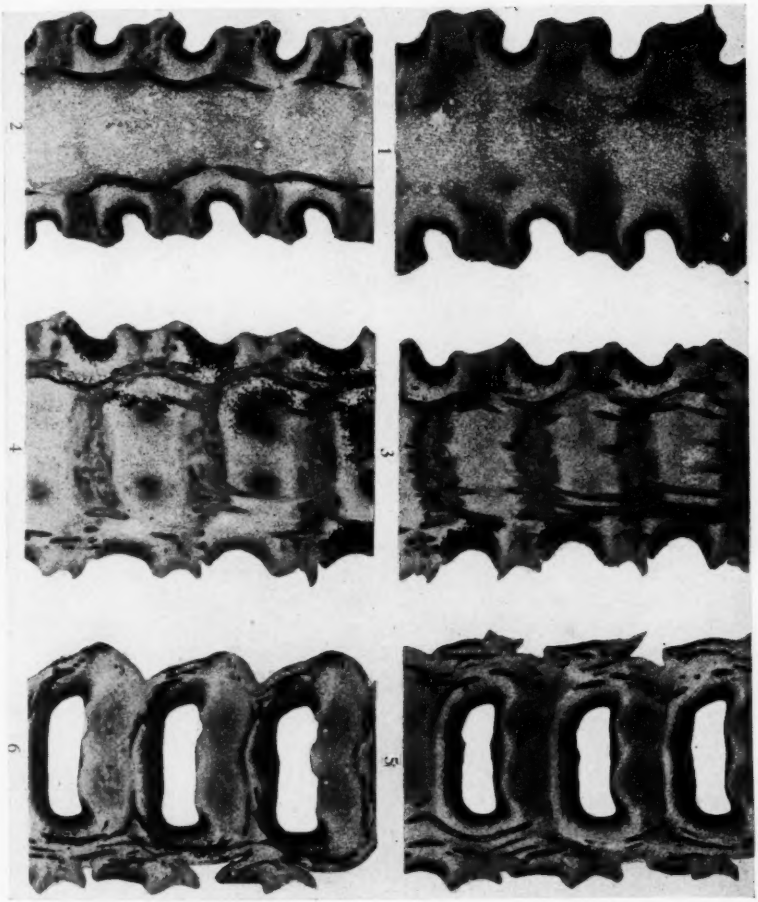
Fig. 2. Sclerenchyma surrounding cupules at side of section. The large vascular strands belong to the inner vascular system, and the small bundles between the large strands belong to the outer vascular system.

Fig. 3. Nodes of rachis show the anastomosing of the vascular strands which pass through the second node without branching.

Fig. 4. Nodes of rachis can be seen and at the sides the beginnings of the next cupules which will be at a 108° angle from the cupule shown in fig. 6.

Fig. 5. Strands of vascular tissue can be seen at side of cupule opening.

Fig. 6. Dark area above and to the sides of the opening of the cupule is heavy sclerenchyma. Gray circular areas below openings are vascular strands of the spikelet surrounding the branched sclerenchyma.



LENZ—HISTOLOGY OF THE CORN COB

THE ROLE OF POD CORN IN THE ORIGIN AND EVOLUTION OF MAIZE

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THE POD-CORN HYPOTHESIS

The hypothesis which holds that cultivated maize has been derived from a wild form of pod corn at one time indigenous to the lowlands of South America is at once the oldest and among the youngest of the various propositions which have been developed to explain the origin of this unique New World cereal. More than a century ago the French naturalist, Saint-Hilaire (1829), described as a new variety *Zea Maïs* var. *tunicata*, a peculiar type of maize sent to him from Brazil in which the grains were covered by the glumes. He concluded that this was the natural state of maize and that South America (Paraguay) was its native home. Virtually all students of maize since Saint-Hilaire have given serious attention to pod corn, have recognized its primitive characteristics, and have either accepted it as the ancestral form, or, for a variety of reasons, have dismissed it from this role. Their viewpoints and conclusions are reviewed and discussed in detail by Mangelsdorf and Reeves (1939). Here it will suffice to set forth the principal reasons given by various students who dismissed pod corn as the ancestral form of maize: (1) it does not breed true; (2) it apparently arises spontaneously in cultures of normal maize; (3) it is frequently monstrous; (4) it differs from normal maize primarily by a single gene; (5) the hypothesis that teosinte is the ancestral form of maize is a more plausible one.

Of the five reasons given for rejecting the pod-corn hypothesis the last is particularly important, for, once the close relationship of maize and teosinte was widely recognized, the pod-corn hypothesis was relegated to a distinctly secondary role. Only recently has it again been brought into prominence by Mangelsdorf and Reeves (1939) who, on the basis of experimental evidence, concluded that teosinte, far from being the progenitor of maize, is instead the progeny of the hybridization of maize and *Tripsacum*. Having dismissed teosinte as the ancestral form of maize, they turned to the earlier pod-corn hypothesis as the only plausible alternative.

The present paper is concerned not with the entire problem of the origin of maize but primarily with the pod-corn hypothesis, and particularly with a mass of new experimental evidence and new observations accumulated during the past ten years which have a bearing upon the problem of the role of pod corn in the origin and evolution of maize. Data previously published are included only to the extent that they are needed in presenting a complete picture; and the extensive literature on pod corn is reviewed only to the extent of providing an adequate background for the present discussion. For more detailed reviews of the literature on pod corn and for earlier data the reader is referred to Sturtevant (1899), Weatherwax (1935), and Mangelsdorf and Reeves (1939).

THE HISTORY AND DISTRIBUTION OF POD CORN

Early History References.—

Since the early history of pod corn has been adequately treated by Sturtevant (1899) there is no necessity for including a detailed review here, and only those references which appear to be highly significant to the pod-corn hypothesis are mentioned. The four references to pod corn which appeared in the first third of the nineteenth century seem to me to be especially important. These are: Azara (1809), Dobrizhoffer (1822), Saint-Hilaire (1829), and Bonafous (1836). All deal with pod corn in South America and three of them with pod corn in Paraguay. Two of them, significantly, speak of pod corn as *bisingallo* or *pinsingallo*, words undoubtedly related to the modern words *pisingallo, passankalla, pisincho, pisinga,* and *piksenkella* which Parodi (1935) and Granado (1931) have listed as being used in South America for varieties of pop corn. Mangelsdorf and Reeves (1939) have pointed out that the use of the word *pinsingallo* in connection with pod corn in the nineteenth century and the use of its derivatives in connection with pop corn in the twentieth century is quite consistent with the conclusion first clearly stated by Sturtevant (1894) that primitive corn was both a *pod* corn and a *pop* corn.

Experimental Verification of an Historical Reference.—

Especially significant to the pod-corn hypothesis and of particular interest in connection with the conclusion that primitive corn was both a pod corn and a pop corn is Azara's (1809) description of the fourth kind of maize which he encountered in Paraguay. Since this description has been quoted in full elsewhere (Mangelsdorf and Reeves, 1939), it need only be said here that Azara described a variety of maize bearing covered seeds in the tassel. This corn was utilized by heating the tassel in oil, whereupon the kernels, still attached to the tassel, exploded to produce, in Azara's own words, a "superb bouquet capable of adorning at night the head of a lady."

By crossing pod corn with pop corn and by backcrossing the hybrid to pop corn for several generations it has been possible to produce a corn which is both pod corn and pop corn and which dipped in hot oil behaves precisely like the fourth variety described by Azara. This simple experiment is not proof that Azara was describing a primitive form of corn. It does prove, however, that what he described *could* have been a pod-pop corn. And since the third variety of corn which Azara described was obviously pod corn there is little doubt in my mind that Azara has given us a description, remarkably picturesque and vivid, of a primitive homozygous pod corn whose seeds were not only covered but also were small, hard, and capable of popping.

Present Occurrence of Pod Corn.—

During the second two-thirds of the nineteenth century, pod corn was repeatedly reported from various parts of North America. It is difficult to determine the significance of some of those reports since pod corn came to be regarded as an interesting curiosity and was actually sold as a novelty by seedsmen (Sturtevant, 1899). Even today it is still passed from person to person and grown as a curiosity so that its occasional spontaneous appearance in open-pollinated fields is of no significance from the standpoint of proving recurrent mutation.

Much more significant, I think, is the possession of pod corn by native peoples. Parker (1910) stated that pod corn was among the varieties grown by the Mohawk and Iroquois Indians and that by the latter it was regarded as sacred. Pod corn occurs in Mexico. I have never encountered pod corn in the field in Mexico but Ing. Eduardo Limón and Ing. Edmundo Taboada of the Dirección de Agricultura in Mexico both have told me that pod corn exists in Mexico, and it has been reported by Khankhoje (1930). There are also ears of pod corn of uncertain origin on display in the local museum near the pyramid of Teotihuacán.

Pod corn is widely known in South America. Contrary to Cook's conclusion (cf. Collins, 1917) that pod corn is unknown in Peru and that there are no words for it in the Quichua vocabulary it can now be said that pod corn, although not common, is well known not only in Peru but also in Bolivia, Ecuador, and Colombia, and that there is a well-recognized term *paca sara* meaning "hidden maize" to describe it. Cutler (1944) has made several collections of pod corn in Bolivia and has made the interesting suggestion that it has been kept in existence and distributed far and wide by the Callahuayo itinerant medicine men. Pod corn of several distinct types, one of which is illustrated in pl. 43A, has been sent to me by Professor Cesar Vargas from Peru. Dr. Arthur G. Kevorkian has told me that pod corn is grown for its magical properties in Zamora, Ecuador, and Dr. Fernando Villamil of the Agricultural Experiment Station at Palmira, Colombia, has informed me that pod corn is well-known in several localities in Colombia. Brieger (1945) has described a form of pod corn from Brazil.

Pod Corn in Prehistoric Maize.—

There is at least one authentic specimen of prehistoric pod corn in the Museum of Northern Arizona at Flagstaff, mentioned by Cutler (1944). The ears of pod corn in the Museum at Teotihuacán in Mexico, already mentioned above, are said to be prehistoric but the evidence is not conclusive. In addition, there are a number of prehistoric ceramic replicas of corn ears which *may* represent pod corn. One of the most convincing is the specimen in the Peabody Museum of Yale University illustrated by Mangelsdorf and Reeves in their fig. 92. Another from the same museum which may be, but certainly is not necessarily, pod corn is illustrated in their fig. 15. Several of the representations of maize on early Peruvian pottery at the American Museum of Natural History show at least external resemblances to pod corn (Mangelsdorf and Reeves, fig. 16). Finally there is a specimen in

the Museum of the University of Pennsylvania which might easily be taken as representing pod corn.

The probability that some or all of these prehistoric specimens were intended to represent pod corn has been enormously increased by the discovery, described elsewhere in this paper, that many of the actual ears of prehistoric corn still in existence are a weak form of pod corn.

THE NATURE OF POD CORN

Genetic Nature.—

Genetically, pod corn, or "tunicate" as it is commonly known among maize geneticists, is the phenotypic expression of a single gene *Tu* located in the long arm of chromosome 4. The *Tu* gene is strongly but not wholly dominant. It always manifests itself in the heterozygous condition but two doses of the gene usually produce a greater effect than one. The *Tu* gene is responsible for producing the principal effects which are characteristic of pod corn, but the degree to which these effects manifest themselves is strongly influenced by modifier factors which are undoubtedly distributed over several chromosomes and probably over the entire chromosome complex.

Morphological Nature.—

The expression of the *Tu* gene varies with the environment and with the background of modifying factors, but the gene is one which usually has manifold effects. Those most commonly recognized are described below:

Glumes:—The principal characteristic of pod corn is that the glumes, which in ordinary corn are reduced to inconspicuous bracts, are completely functional and, as in other cereals, enclose the caryopsis. There is enormous variation in the degree to which the glumes develop. In some ears they are monstrous; in others they scarcely enclose the grain. On any one ear of pod corn the glumes are usually more strongly developed at the base of the ear than at the tip. The reason for this is not known.

The *Tu* gene affects not only the glumes of the pistillate spikelets but also the glumes of the staminate spikelets in the tassel. This second effect is less noticeable than the first since the staminate spikelets already normally have glumes completely enclosing the floral structures. Nevertheless, it is usually possible to distinguish tunicate or heterozygous tunicate plants from non-tunicate plants in the same family by the size of the glumes on the staminate spikelets.

Another characteristic of the glumes of pod corn is that they are membranaceous or papery rather than indurated or horny. In this respect pod corn differs not only from teosinte and *Tripsacum*, the closest relatives of maize, but also from most varieties of *Coix* and of *Sorghum*. Membranaceous glumes are not, however, unique to pod corn since they are characteristic of many grasses.

Staminate and Pistillate Spikelets:—The second most conspicuous effect of the *Tu* gene is evident in the terminal inflorescence or tassel. This structure, normally

wholly staminate in the majority of modern corn varieties, becomes partly pistillate in the presence of the *Tu* gene, sometimes in plants heterozygous for the gene, almost always in plants homozygous for it.

The transformation of a staminate inflorescence to a partly pistillate one may occur in various ways. Dissection and examination of several thousand florets in the tassels of *TuTu* and *Tutu* plants have led to the following observations:

1. Florets on a mixed inflorescence may be: (a) functionally pistillate; (b) functionally staminate; (c) perfect; (d) functionally pistillate with visible but non-functional anthers; and (e) abortively staminate.

2. Pistillate or perfect florets are most common in the lower spikelets on the tassel branch, but are not confined to them.

3. If both florets in a single spikelet develop, both may be staminate (common), both pistillate (rare), the upper pistillate and the lower staminate (rare), or the upper perfect and the lower pistillate (common).

4. If only one floret in a spikelet is pistillate, it is invariably the upper.

5. If only one floret in a spikelet is perfect, it is invariably the upper.

6. When pistillate, perfect-flowered and staminate spikelets all are found on the same branch, the pistillate are likely to occur below, the staminate above, and the perfect-flowered between.

The degree to which the tassels of pod corn become pistillate, like the development of the glumes, varies with the environment and the genetic background. There is, however, a strong correlation between glume development and sex-reversal in the tassel. Heterozygous tunicate plants which are strongly pistillate in the tassel are almost certain to have prominent development of glumes on the ear, when there is an ear.

If the terminal inflorescence, or tassel, is strongly pistillate, then the lateral inflorescence, or ear, is likely to be suppressed. This is probably a simple matter of the amount of plant nutrients available, and the fact that the terminal inflorescence apparently has priority in its requirements. It is usually possible to induce the formation of an ear in a tunicate plant which would otherwise be earless by removing the tassel soon after it emerges.

Secondary Pistillate Florets:—The tunicate condition is often, but by no means always, accompanied by the development of secondary pistillate florets. This may occur either in the tassel or in the ear. An example of the latter is illustrated in pl. 45C. This condition, which is a genetic one in the sweet corn variety, Country Gentleman, is in tunicate maize undoubtedly the consequence, at least in part, of the release which the tunicate condition provides from compaction and pressure. This is suggested by ears which have elongated beyond their husks. On such ears, spikelets with the lower floret developed occur almost invariably in the region not compressed by the husks.

Branching of the Ear:—In some stocks, notably in my crosses of pod corn with the Guarany maize of Paraguay, the tunicate condition is often accompanied

by basal branching of the ear. Since the basal branches are two-ranked, they contribute toward producing a structure which, except for the fact that it is pistillate rather than staminate, is the exact counterpart of the tassel, a polystichous central spike with distichous basal branches. An ear of this type is shown in pl. 44.

Basal branching of the ear, like the development of secondary florets, is probably in part a response to release from compaction.

Elongation of the Rachis:—One of the most conspicuous effects of the tunicate gene, and one whose consequences have already been described in part, is a release of the strong compaction characteristic of the normal modern ear of corn, which, as I have pointed out elsewhere (1945), is a strongly compacted structure. The extent to which compaction is released, like other effects of the *Tu* gene, varies with the environment and with the genetic background. In some stocks, again notably in crosses of pod corn by Guarany maize, the ear grows far beyond the husks and becomes so lax that its true nature is clearly revealed (pl. 42). The rachis is slender and fragile like the rachises of other cereals. The paired nature of the pistillate spikelets, obscured in many modern varieties of maize, is readily apparent, and in some cases the sessile and pedicellate members of the pair are distinguishable. In some ears of pod corn the whorled phyllotaxy of the inflorescence is also clearly revealed.

Elongation of the "Shank":—Also, sometimes, but by no means always, accompanying the tunicate condition is an elongation of the stalk, commonly known as the "shank," upon which the ear is borne. Here again environment and modifying factors play a part. The most striking example of this elongation which I have encountered occurred in a plant of Guarany pod corn which bore three ears on its main stalk and one ear on each of its three tillers. The ears on the tiller stalks were normal with contracted shanks and normal husk covering, but the three ears on the main stalk all had elongated shanks bearing more or less normal leaves instead of husks at the nodes, and terminating in naked or partly naked ears. This plant is an excellent demonstration of the widely accepted conclusion that the ear of maize is the terminal inflorescence of a lateral branch which has become drastically contracted and that the husks are leaf sheaths arising from each node which have largely lost their leaf blades and which because of the contraction of the branch have become strongly overlapping. This plant also demonstrates that all of these profound changes can occur spontaneously and almost as a single step. In this instance the tunicate gene has apparently brought the plant to a threshold where slight differences in the environment (the kind of difference in environment which exists between the main stalk and the tillers) may have drastic and dramatic effects.

Other Effects: How many other effects the *Tu* gene produces remains to be determined. Preliminary investigations by Prat (reported in a conversation)

indicate that the epidermal characteristics of tunicate maize are different from those of non-tunicate maize and are of a category which he regards as primitive for the grasses. There is little doubt that still other differences between tunicate and non-tunicate maize will be found when more intensive morphological studies have been made.

Effect of Tu on Teosinte.—

Brieger (1944) is of the opinion that the spikes resulting from crossing teosinte and pod corn followed by backcrossing to teosinte provide an experimental reconstruction of wild corn. I do not share that opinion. It is clear, however, that such crosses can shed light not only on the morphological nature of teosinte but also on that of pod corn.

Certain effects of pod corn are emphasized and clearly revealed when the *Tu* gene is introduced into varieties of teosinte by hybridization of pod corn and teosinte, followed by repeated backcrossing to teosinte. Fruits of tunicate teosinte compared with fruits of normal teosinte are illustrated in pl. 46. In normal teosinte the fruit case comprises an indurated glume of restricted proportions plus an indurated rachis segment which internally is concave and partly surrounds the caryopsis. In tunicate teosinte the caryopsis is completely enclosed by prominent, membranaceous glumes, and the rachis segment becomes nothing more than an appendage[1], playing no part in enclosing the caryopsis. These two fruit cases, so different that if encountered in nature they would undoubtedly be assigned to different species if not to different genera, are the products of the two genes *tu* and *Tu*. The segregation of the two types is approximately 1:1 in backcrosses of the heterozygote to the recessive. This fact may be of considerable significance in the study of the world's corn varieties. It is almost certain that varieties of corn originating from a strong introgression of *Tripsacum* into maize, either directly or through contamination of maize by teosinte, would have quite a different cob anatomy from those originating directly from any kind of tunicate maize. The former, which we may call "tripsacoid," would be a compound structure made up of individual units fundamentally like the fruit case of normal teosinte, but modified by crowding and pressure. Such a cob would be expected to have a thick, stiff, and indurated rachis with distinct rachis cavities from which arise spikelets whose outer glume is reduced to an indurated bract. On the other hand, a cob derived from a tunicate or weak tunicate maize, which we may call "tunicoid," would be expected, since it is made up of units fundamentally like the fruit case of tunicate teosinte, to have a slender, flexible, or fragile rachis, with the spikelets arising from its surfaces partly enclosed in membranaceous glumes.

There is no doubt that maize varieties possessing these two kinds of cobs exist. And since stocks with the indurated rachis and glumes of teosinte can be produced by controlled introgression of teosinte into maize there is little doubt that some

[1]None of the fruits of tunicate teosinte in my cultures resemble those illustrated by Brieger in which the rachis remains intact and separation occurs at the base of the grain.

maize varieties of this type have arisen through such introgression. On the other hand, since the two types of teosinte described above differ primarily by a single gene it is possible that a tripsacoid type of maize ear, or something approaching it, can result from a simple mutation of *Tu* or one of its alleles to *tu* in a tunicoid type.

Most of this is obviously highly speculative and is included here only because it suggests some of the problems to which pod corn seems to hold at least one of the keys.

The Primitive Nature of Pod Corn.—

Many, if not all, of the effects of the *Tu* gene result in conditions which have been recognized as primitive by students of maize and its relatives. That wild corn must have had its grains enclosed in glumes has been noted by virtually all students of maize. That the ear is the terminal inflorescence of a drastically contracted lateral branch is widely accepted. That the husks are overlapping leaf sheaths minus the leaf blades is scarcely a matter for dispute. That the ear is the counterpart of the central spike of the tassel and is similar to a tassel minus its basal branches has been pointed out by several writers. Hence, in all of these features the *Tu* gene has the *tendency* to restore a condition which was undoubtedly characteristic of primitive maize.

It is possible, but not certain, that the tendency of tunicate maize to develop perfect-flowered spikelets and secondary pistillate florets also represents a reversion to a more primitive condition. It is generally recognized that the remote ancestor of maize and its relatives must have been perfect-flowered. But since *Tripsacum* and teosinte, the closest relatives of maize, are monoecious rather than perfect-flowered, I am inclined to believe that the occurrence of perfect-flowered spikelets in the tassels of tunicate maize represents a transition from a wholly staminate condition to one in which, as in *Tripsacum*, there are staminate and pistillate spikelets borne more or less separately on the same branches. The evidence for this, in so far as there is any evidence in tunicate maize, lies in the fact that inflorescences which are wholly perfect-flowered are never found. Perfect florets occur only in mixed inflorescences and are often found between a part of the branch bearing mainly pistillate florets and one bearing mainly staminate florets.

The significance of secondary pistillate florets in pod corn is even less clear. As already suggested, they may be nothing more than the consequence of a release from compaction. On the other hand, since the development of both florets is undoubtedly primitive in the grasses and since there are varieties of maize such as Country Gentleman in which the development of both florets is the rule rather than the exception, I suspect, although I certainly cannot prove, that the development of both florets in pod corn represents a tendency to revert to a condition characteristic of primitive maize. In this connection it is of interest to note that Dr. Cutler collected in the same village in Bolivia ears of tunicate maize and ears of maize which were not only branched but also bore secondary pistillate florets.

Leaving open the question of the significance of perfect florets and secondary pistillate florets in pod corn it is still obvious that the *Tu* gene is one which has a tendency to restore, not only the universally recognized primitive characteristic of glume-covered seeds, but an entire complex of primitive characteristics as well.

NEW GENETIC EVIDENCE ON POD CORN

True-breeding Pod Corn.—

One of the recurrent objections to the pod-corn hypothesis is that pod corn does not breed true. Homozygous pod corn, when it occurs in the cultures of the geneticist, is usually pollen-sterile and hence incapable of reproducing itself. It has already been pointed out (Mangelsdorf and Reeves, 1939) that this objection is not necessarily valid, since, if pod corn were the primitive type, then the *Tu* gene of today is a relict "wild" gene superimposed upon a genetic background frequently lacking in the background of modifiers which once kept the character under control. In the absence of these controlling modifiers the tunicate character would be expected to result frequently in monstrous development of the glumes accompanied by partial or complete sterility. This sterility is sometimes structural and sometimes probably physiological. Structural sterility exists when functional anthers are formed which, because of the sheer massiveness of the glumes surrounding them, are incapable of becoming exserted. Sterility thought to be of a physiological nature occurs when the glumes are so monstrous and demand so much energy in their development that, as a result, both male and female reproductive organs are abortive. In any case, there is great variation in the development of the tunicate character, and, as I previously pointed out (1947), there seemed to be a possibility of producing a completely fertile form of pod corn either by (a) selecting for restraining modifying factors or (b) substituting for the modifier complex of present-day pod corn a more ancient complex obtained from a primitive variety.

In a previous paper (1947) I reported that an experiment involving selection for minus modifiers of pod corn had been brought to a successful conclusion. I must now modify that statement, for although I did succeed in producing a number of true-breeding lines of pod corn by selection for minus modifiers, the extreme form which I described and illustrated has since proved to be the product not only of the accumulation of minus modifiers but also of a new allele at the *Tu-tu* locus. This new form of pod corn is described in some detail later in this paper. Homozygous forms of pod corn involving the original allele have much more prominent glumes than the new form illustrated in my previous paper (1947).

The other experiment previously reported, which sought to develop a true-breeding pod corn by introducing the modifier complex of a primitive variety, has not yet been completed. There is no doubt that the Guarany maize from Paraguay which was used in this experiment possesses modifiers capable of restraining the tunicate character. Furthermore, homozygous tunicate plants derived from

this experiment which are both male-fertile and female-fertile have been observed. There is little doubt, therefore, that a homozygous true-breeding form of pod corn will be produced in due time as a consequence of introducing modifiers of the tunicate character from a primitive variety.

Alleles of Pod Corn.—

As already mentioned, the attempt to produce a true-breeding pod corn through selection for minus modifiers resulted in the discovery of a new allele of *Tu*. The circumstances were as follows: in 1942, in a population derived from self-pollinating a *Tutu* plant during the previous season, one plant was found which not only appeared to be homozygous tunicate, bearing pistillate spikelets in the tassel in profusion, but was also male-fertile. This plant was self-pollinated in the tassel and gave rise in the following generation, which was grown in 1944, to a population of 64 plants, all of which were tunicate. A number of these were self-pollinated and in addition were crossed on various inbred strains, primarily A158 and P39, in order to provide a final test for homozygosity for *Tu*. The crosses thus produced were grown in the season of 1945. Some of these F_1 crosses were so weakly tunicate that they appeared at first glance to be non-tunicate. This weakly tunicate condition was thought at the time to have been the consequence of selection for minus modifiers, but it has since become apparent that the new pod corn involves not only minus modifiers but a new allele of *Tu* which has apparently arisen spontaneously in the course of these experiments. The existence of this allele was first indicated when one of the crosses made to test homozygosity gave rise to strongly tunicate and weakly tunicate plants in a ratio of 8 to 5. The results were verified by repeating a planting of the same cross in 1946 when 10 strongly tunicate and 15 weakly tunicate plants were counted. A third planting in 1947 yielded the two types in a ratio of 8 to 4. The ratio in the total population is 26 strongly tunicate and 24 weakly tunicate. Obviously, the plant selfed in 1944 which furnished the pollen of this cross was either heterozygous for two alleles of *Tu* or was segregating for a major modifier of this gene. The first explanation is now known to be the correct one. Since the weaker form of tunicate produces approximately the same effect when homozygous as does the stronger when heterozygous, it may appropriately be designated as "half-tunicate," and assigned the symbol tu^h. It is illustrated in pl. 47.

Since this cross had been made on the inbred P39 which is pure for sugary, a gene on the fourth chromosome, a further test for allelism was easily made by backcrossing the hybrid to a sugary stock. Plants of two such backcrosses, one with a tunicate hybrid as one parent, the other with a half-tunicate parent, were grown in the summer of 1948 with the following results. The backcross of sugary to the strongly tunicate hybrid yielded four classes in the numbers shown:

Starchy tunicate	32	
Starchy non-tunicate	14	37 crossovers = 38 per cent
Sugary tunicate	23	
Sugary non-tunicate	29	

The backcross of sugary to the heterozygous half-tunicate yielded four classes in the following numbers:

Starchy half-tunicate	34	
Starchy non-tunicate	16	28 crossovers = 30 per cent
Sugary half-tunicate	12	
Sugary non-tunicate	32	

The results are in harmony with the assumption that the strong and weak forms of tunicate are due to different alleles of *Tu*.

Are There Modern Varieties of Pod Corn?—

Once it was suspected that half-tunicate is an allele of tunicate, the questions at once arose: Are there still weaker alleles of *Tu*? And are there modern varieties of maize which are in reality weak forms of pod corn? An examination of the ears in my collection indicated at once that there are living varieties which give the impression of being weak pod corn. The cobs are flexible and the caryopses are partly covered by membranaceous glumes. In some varieties these glumes are sufficiently developed to almost enclose the seeds, particularly toward the base of the ear where the glumes of pod corn are, as already mentioned, usually most prominent.

The assumption that these types are actually weak forms of pod corn is verified by linkage data. In 1947, for example, there was available in my cultures a population of plants resulting from a cross of a Guatemalan variety, No. 16, with the sweet corn variety, Country Gentleman. The cross had been made to study the linkage relations of pilosity, and the starchy and sugary seeds had been planted separately. When it was discovered that the variety Guatemala 16 appeared to be a weak form of pod corn, a classification of weak-tunicate and non-tunicate was attempted. The difference between them was manifested more strongly in the stiffness and flexibility of the cob than in the glumes themselves. Two classifications, one made by the writer and the other made completely objectively by an assistant who, unaware of the problem involved, merely classified the ears as stiff or flexible, yielded the following results:

	Classified by PCM	*Classified by LMJ*
Starchy; flexible	18	21
Starchy; stiff	9	6
Sugary; flexible	6	12
Sugary; stiff	25	19
	58	58

In spite of the discrepancies, there is in both classifications a definite association between starchy endosperm and flexible cobs and sugary endosperm and stiff cobs. If we suppose that flexibility represents one manifestation of a weak form of tunicate, which we may designate as tu^w, then the two middle classes above represent crossovers between *Su* and tu^w and *su* and *tu*. In the first classification these comprise 26 per cent of the total; in the second, 31 per cent. Both figures are remarkably close to the 29 per cent of crossing over which normally occurs between *Su* and *Tu*. We have, therefore, a strong indication that the flexibility which is characteristic of the cob of Guatemala No. 16 is actually a weak form of tunicate.

Two additional backcross populations of this type, one involving a Guatemalan and the other a Nicaraguan variety, were grown in 1948. Distinct variation occurred in both populations but was more apparent in the fragility of the cob than in its flexibility, perhaps because the ears had been more completely dried than those grown in 1947. In any case, it was possible to separate the ears into two distinct classes, fragile and solid, on the basis of the ease with which the cobs were snapped in two. The results of such a classification are as follows:

	Family 1583	Family 1585	Total
Starchy; fragile	33	31	64
Starchy; solid	12	15	27
Sugary; fragile	18	12	30
Sugary; solid	25	31	56
	88	89	177

If we assume that fragility of the cob is due to a weak tunicate allele of tu^w then the two middle classes, starchy; solid, and sugary; fragile, represent crossovers. These comprise 32 per cent of the total. Considering the small size of the sample, this is remarkably close to the approximately 29 per cent expected if fragility is the result of a weak allele of *Tu*.

These combined data strongly indicate that the three varieties involved in these crosses were weak-tunicate and they also indicate that the gene for this condition has its locus on the fourth chromosome approximately 30 crossover units from *Su*, exactly where an allele of *Tu* would necessarily have its locus.

Genetic Tests for Alleles of Tu.—

A corollary of the assumption that fertile forms of pod corn can be produced by introducing controlling modifiers from primitive varieties is that the farther removed a variety becomes from its center of origin and its original pod-corn ancestor, the fewer controlling modifiers it will have retained. Hence, if maize originated from a wild pod corn once indigenous to the lowlands of South America, we should expect to find controlling modifiers of pod corn in highest frequency in South American varieties and in lowest frequency in the United States.

To test this assumption, 116 varieties and inbred strains of corn from eight

Latin American countries and from various regions of the United States were crossed on a uniform inbred strain of half-tunicate. The ears of the F_1 hybrids were then studied and classified with respect to the development of the tunicate condition. There was, as expected, considerable variation in the development of the glumes in the F_1 hybrids ranging from those in which the glumes were not visible unless the grains were removed, to those in which the glumes completely covered the seed. The ears were arbitrarily divided into four classes on the basis of a "glume score" defined as follows:

Glume Score	*Definition*
1	Glumes scarcely apparent.
2	Glumes apparent but do not cover grains.
3	Glumes cover grains on lower part of ear.
4	Glumes cover practically all grains.

When these glume scores were averaged for different countries, and for different areas of the United States (cf. Table I), there proved to be, as had been anticipated, consistent regional differences. But the results were *exactly the reverse* of those predicted. Crosses with South American varieties which were expected to have the lowest glume scores because of controlling modifiers of the tunicate condition had the highest glume score, while varieties from the United States, expected to be highest in glume score, were lowest.

TABLE I

AVERAGE "GLUME SCORES" IN F_1 HYBRIDS OF MAIZE VARIETIES AND INBRED STRAINS WITH AN INBRED STRAIN OF POD CORN

Country, State, or Group	Number of varieties	Glume score
Paraguay	3	3.7
Bolivia	3	3.3
Brazil	2	2.0
Nicaragua	3	3.0
Costa Rica	1	3.0
Mexico	35	2.9
Cuba	3	2.8
Guatemala	6	3.4
Texas	9	2.2
North Carolina	6	2.8
Corn-Belt	17	1.5
Minnesota	10	1.8
Wisconsin	5	2.0
U. S. Sweet Corn Varieties	13	2.1
Av. South America	8	3.1
Av. Central America & West Indies	48	2.9
Av. United States	60	2.0

When an experiment, as in this case, yields results exactly the reverse of those anticipated, it does not mean that the experiment is a failure or that the inductive reasoning which led to it is entirely fallacious. On the contrary, the fact that an experiment yields conclusive results, even if in the "wrong" direction, indicates that the basic premise upon which it rests must have some validity. In this case, the basic premise that South American and North American maize varieties differ in their ultimate relationship to pod corn is undoubtedly valid. But the assumption that this difference is primarily one of modifiers affecting the tunicate conditions is not established. Undoubtedly there are modifiers affecting the tunicate condition; indeed, this fact is easily demonstrated. Perhaps it is even true that controlling modifiers of tunicate have a higher frequency on the average in South American varieties than in North American, but if so, the fact is not established by this particular experiment. What this experiment demonstrates, I think, is that South American and North American varieties of maize differ primarily not in modifiers of tunicate, but in weak alleles of tunicate. When the inbred strain of half-tunicate, tu^h, is crossed with a variety homozygous for weak tunicate, tu^w, then the F_1, $tu^h tu^w$, might well be expected to have stronger glumes than an F_1, $tu^h tu$, resulting from a cross with a non-tunicate variety *tu*.

On this assumption the results in Table I become completely intelligible in terms of the pod-corn hypothesis and are completely in harmony with it. South American varieties have the highest average glume score presumably because weak alleles of *Tu* have their highest feequency in South America. Central American varieties are intermediate in glume score, and United States varieties lowest. Within the United States the strains of the Corn-Belt proper have lower glume scores than those of any other part of the United States.

The regional differences in glume scores of these F_1 hybrids is strongly correlated with the morphological appearance of the cobs of the parental varieties. The frequency of cobs with "pockets" and the alveolate appearance characteristic of weak pod corn is high in Paraguay, Bolivia, Peru, Ecuador, Colombia[1], Costa Rica, and Guatemala. It is less high in Mexico and the West Indies, and is lowest in the inbred strains of the Corn Belt of the United States. Ears with alveolate cobs from Peru, Colombia, and Mexico are compared with an ear known to be heterozygous for half-tunicate in pl. 48.

The correlation is by no means complete, however, for two varieties which are identical in appearance with respect to the development of glumes may produce quite different hybrids when crossed with tunicate. Furthermore, two varieties whose hybrids with tunicate are identical in glume score may themselves be quite different in appearance. These discrepancies can be attributed to modifier

[1]So far as external appearance alone is concerned weak pod corn seems to have its highest frequency in Colombia. This is the only new evidence which I have encountered which supports the conclusion of Birket-Smith (1943) that maize had its origin in Colombia. Cutler (in press) has criticized the linguistic evidence on which Birket-Smith's conclusion is largely based but the evidence from pod corn lends new significance to it. The question of whether maize originated in the Paraguay-Bolivia region or in Colombia is still open but the conclusion that it originated in South America has become almost a certainty.

complexes superimposed upon allelic differences. There is little doubt that both are operating.

But whether the regional differences revealed by this experiment are the result of differences in tunicate alleles, in modifier complexes, or in both, the fact remains that there are consistent differences. This is itself highly significant with respect to the pod-corn hypothesis, for if pod corn is not an ancestral form, if it is simply a mutant which has arisen spontaneously again and again in the history of maize under domestication, then there is no reason why "clines" with respect to genetic factors affecting its expression should exist. The very fact that there are such clines is a strong indication that pod corn has had a role in the evolution of maize.

Additional evidence that both modifiers and alleles of *Tu* are involved in Latin American maize varieties can be obtained by backcrossing to the parental strain of half-tunicate their F_1 hybrids with half-tunicate. If a Latin American variety is *tutu*, then the F_1 hybrid is $tu^h tu$ and the backcross to half-tunicate, $tu^h tu^h$, should yield two genotypes, $tu^h tu^h$ and $tu^h tu$, in equal numbers. These two genotypes should be readily distinguishable but if modifiers are involved there should be noticeable variation within each class. On the other hand, if a Latin American variety being tested is weak tunicate, $tu^w tu^w$, then the two classes in the backcross are $tu^h tu^h$ and $tu^h tu^w$. These should be less easily distinguishable than the two classes expected in the first instance, and, if modifying factors are also involved, the variation within each class might well result in an overlapping of the two classes to the extent that the two genotypes cannot be accurately separated.

Populations from eight backcrosses have been grown involving two varieties each from Mexico and Nicaragua and four from Guatemala. Four of these yielded two distinct classes with marked variation in each class but with no overlapping. In the remaining four, distinct classes did not occur. There was marked variation in the development of the glumes but it was not possible to separate the ears with complete accuracy into two distinct classes. It seems reasonable to conclude that modifiers of *Tu* were involved in all crosses but that the Latin American varieties entering into the first four crosses were of the genotype *tutu* while in the last four crosses they were $tu^w tu^w$.

MUTABILITY OF *TU* AND ITS ALLELES

As already mentioned, the weak allele of *Tu* now designated as half-tunicate, tu^h, occurred spontaneously in my cultures involving *Tu*. Since the total number of tunicate plants grown in cultures in which mutations could be detected did not exceed several hundred, it is obvious that *Tu* is either a mutable gene or the sample represented by my cultures is not a random one. Other data are available to indicate that the first explanation is at least in part the correct one.

In the fall of 1946, when harvesting ear-rows of a stock developed originally by crossing pod corn with the Guarany maize of Paraguay and backcrossing repeatedly to the Guarany variety, I discovered one ear heterozygous for *Tu* which was a chimera with respect to the tunicate and non-tunicate condition. Approxi-

mately three-fourths of the ear bore seeds enclosed in glumes while the remainder, comprising one side and the entire tip of the ear, bore naked or partly naked seeds. The ear is illustrated in pl. 45A. Seeds from the two portions were planted separately in 1947 with the results shown below. The ear found in 1946 was open-pollinated so that outcrosses occurred in the progeny. These could, however, be distinguished from plants resulting from selfing or sibbing. The distribution of the progeny from the two portions of the same ear is as follows:

	Outcrosses		*Selfs or Sibs*		
	Tutu	*tutu*	*TuTu*	*Tutu*	*tutu*
Tunicate portion	0	3	4	3	1
Non-tunicate portion	0	4	0	2	4

The data, though not extensive, prove that the parent ear was heterozygous for *Tu*, and they strongly indicate that the ear was also a chimera with respect to the two kinds of somatic tissue *Tutu* and *tutu*. The indications are twofold. First, all of the outcrosses, seven in number, proved to be *tutu*. Had the parent ear been of the composition *Tutu* throughout, then the outcrosses should have comprised genotypes *Tutu* and *tutu* in equal numbers. The odds against all being *tutu* are 127:1. Secondly, the distribution of the three genotypes among the selfs and sibs is almost, though not quite, significantly different in the progenies from the two portions of the ear. Both of these facts are in harmony with the assumption that the parent ear was a chimera of *Tutu* and *tutu* tissue, and combined they lend a high degree of plausibility to that assumption. If this is indeed the case, then this represents a second mutation from *Tu*, this time to the allele *tu*, which has occurred in my cultures in the past ten years.

A controlled experiment on mutability involving the allele tu^h rather than *Tu* was conducted in 1947 and 1948. Plants of the inbred strain Minn. A158 were crossed by an inbred strain homozygous for two dominant genes, tu^h and *B*, the latter a gene responsible for sun-red plant color. Mutations could be readily distinguished in the progeny from the products of accidental contamination by the fact that the latter were recessive for both genes while mutations were recessive for only one. No mutations occurred in the *B* factor in a population of 2125 plants resulting from this cross while one non-tunicate sun-red plant was found. If this proves, on the basis of a progeny test, to be a mutation and not a phenocopy, then the mutation rate at the tu^h locus as determined by this single sample is 471 per million gametes. This is only slightly less than the rate, 492 per million, which Stadler found at the *R* locus.

So far as I know, the reverse mutation from *tu* to *Tu* has never been observed. True, tunicate plants for which a spontaneous origin has been assumed have sometimes been discovered in ordinary corn fields. Sturtevant (1894) and Sconce (1912) have both reported the appearance of pod corn in non-podded varieties but the circumstances do not rule out contamination in the previous generation, especially since pod corn has been widely grown as a curiosity. On the other hand, millions of ears of inbred strains and single-crosses have been grown in con-

nection with the production of hybrid seed corn in the past twenty-five years and not a single instance of the spontaneous occurrence of pod corn in these pedigreed cultures has been reported,[1] although other mutations, especially to teopod, have been encountered repeatedly. So far as these data are a criterion, they indicate that *Tu* is not a gene which arose recently through spontaneous mutation but is an ancient gene which has survived in the population perhaps for thousands of generations.

THE APPARENT SPONTANEOUS OCCURRENCE OF SOLITARY TUNICATE SPIKELETS

An interesting phenomenon which must certainly have often been observed, but which so far as I know, has never been reported, is the occurrence of one or more solitary tunicate spikelets or pairs of spikelets on ears which are apparently in all other respects non-tunicate. I have now encountered this phenomenon in three separate instances, in a Nicaraguan variety, in a Mexican variety collected by Dr. E. J. Wellhausen, and in an F_1 hybrid of Midget $\times$ P39. In the last case five different ears each bearing one or more tunicate spikelets were found in a population of 39 ears.

In addition to these three cases, I have received from Dr. Isabel Kelly of Mexico, through the kindness of Dr. Edgar Anderson, a single tunicate kernel found on an ear of Mexican maize. Dr. Kelly writes that kernels of this kind are occasionally found and that they are regarded as having magical properties.

All of these instances of the apparent spontaneous occurrence of tunicate spikelets can, I think, be explained as the monstrous development of glumes on weak forms of pod corn. Certainly this is true of the three ears which I encountered, and since weak pod corn is common in Mexico, I have no doubt that it is true of the case reported by Dr. Kelly. Why an occasional spikelet of weak pod corn should suddenly develop strongly tunicate and even monstrous glumes, and why such spikelets are always basal, is not clear. It is a fact, already mentioned, that the glumes of pod corn are usually more strongly developed on the lower spikelets of the ear than on the upper. It is also a fact that strains of half-tunicate corn sometimes develop monstrous glumes on basal spikelets. But whatever the reason for their occurrence the fact that they do occur is convincing visual evidence that weak forms of pod corn are still truly pod corn.

EVIDENCE OF WEAK POD CORN IN PREHISTORIC TIMES

Many of the prehistoric ears of corn from Peru which I have had an opportunity to examine exhibit the alveolate appearance and the deep "pockets" characteristic of the cobs of weak forms of pod corn. Furthermore, their frequency is highest among the ears from the more ancient sites. Two ears from Tello's Paracas collection are illustrated in pl. 45B, and one from his Nazca collection in pl. 48A. There is little doubt, I think, that all represent weak forms of pod corn.

[1] It is possible that ears of pod corn which occur in commercial fields are discarded at processing plants without being reported, but Mr. Ralph Gunn and Mr. R. R. St. John of the DeKalb Agricultural Association have both told me that they have never seen an ear of pod corn in their experimental hybrids. Each has approximately a half-million plants in his tests annually.

A comprehensive study of the prehistoric maize of the Southwest with respect to the presence of weak pod corn has not yet been made. I can only say that many of the ears in the collections of the Peabody Museum of Harvard University have cobs with strongly alveolate surfaces. Also, four ears recently discovered by C. T. Hurst at Cottonwood Cave, Colorado, and sent to me by him for examination have alveolate cobs which closely resemble not only the weak pod corn of modern varieties but also the prehistoric corn of Peru. Dr. Edgar Anderson has kindly given me permission to state here that of twenty-six ears of Basketmaker I corn in the museum at Mesa Verde National Park which were examined by him, eight had prominent glumes. There is little doubt that much, if not most, of the prehistoric corn of both North and South America is weak pod corn.

The facts (1) that the familiar form of pod corn has been found among prehistoric ears; (2) that it, or something curiously like it, is represented in prehistoric ceramic replicas; and (3) that many of the well-preserved ears of prehistoric corn from North and South America are identical in the structure of their glumes and in the alveolate condition of the cobs to modern forms of weak pod corn, represent perhaps the most convincing combination of evidence yet found in support of the pod-corn hypothesis.

THE EARLY EVOLUTION OF MAIZE UNDER DOMESTICATION

The Ancestral Form of Corn.—

In this paper we are concerned only with the early evolution of maize and with the evolutionary paths which it followed before the hypothetical hybridization with *Tripsacum* occurred.

If maize originated from a wild form of pod corn, then we may assume that part or all of the effects now produced by the *Tu* gene contribute toward restoring a primitive or ancestral condition. On the basis of this assumption we can conclude that:

1. Wild corn had its caryopsis enclosed in glumes.
2. The terminal inflorescence bore staminate and pistillate spikelets separately on the same branches, the former below, the latter above, as in *Tripsacum*.
3. Both staminate and pistillate spikelets were paired.
4. The plant bore no "ears" but from the upper nodes arose lateral branches, which, like the main stalk, terminated in a panicle-spike bearing staminate and pistillate spikelets.
5. It is possible, but by no means certain, that the glumes of the pistillate spikelets enclosed two functional florets.

From other evidence we can conclude that:

6. The grains of wild corn were small, flinty, and capable of popping.

There is no way of determining from the evidence (a) whether the plant was an annual or a perennial, or (b) whether branching of the stem was confined to the higher nodes or whether basal branching also occurred. I suspect, largely because there are no perennial forms of maize in existence, that wild corn was an annual.

On the question of basal branching I do not even have grounds for an opinion. Perhaps, as in present-day maize, both high branching and basal branching occurred.

It should be obvious, at least to any student of maize and its relatives, that the plant described above shows a decided resemblance to *Tripsacum*. Indeed, except for its annual habit, its membranaceous glumes, its paired pistillate spikelets, and its central spike, it is virtually identical with *Tripsacum*.

The Change From Wild Pod Corn to Modern Corn.—

If again we assume that wild maize was a form of pod corn, then it is a simple matter to visualize some of the steps involved in its evolution under domestication. Many of the changes which occurred would have been the reverse of those which now occur when the gene *Tu* is superimposed upon a modern variety. On this basis the most important event in the evolution of maize was a mutation in a single gene *Tu*. In the light of the new evidence on *Tu* alleles presented in this paper, we can no longer visualize this as a single drastic change from *Tu* to *tu* (Mangelsdorf and Reeves, 1939). Instead there must have been a series of mutations from higher to lower alleles. In either case, the ultimate effect would have been the same. The glumes became shorter. The lateral branches and their terminal inflorescences became enclosed in overlapping leaf sheaths which largely lost their leaf blades. The lateral inflorescences became pistillate, strongly compacted, and lost their basal branches until only the central spike remained. The terminal inflorescences on the main stalk, the present tassel, became wholly staminate. The caryopsis gradually became larger.

All of those changes initiated by mutations in the *Tu-tu* series which proved to be advantageous to the plant under domestication were accentuated by selection, both natural and artificial, acting upon the genes in the modifier complex so that the ultimate change was considerably greater than that produced by mutations at the *Tu* locus alone.

In following the evolutionary paths which are outlined above, maize has left upon the scene many intermediate forms. This is one important respect in which the pod-corn hypothesis differs significantly from the teosinte hypothesis. If maize originated from teosinte then the intermediate forms which must once have existed are now conspicuously lacking. True, occasional plants are found, as abnormalities, which exhibit the response to short days, characteristic of teosinte, or whose ears are distichous, or whose pistillate spikelets are single; but well-established varieties possessing these teosinte characteristics are unknown. If, on the other hand, maize originated from a wild pod corn then the intermediate forms which must have occurred are still to be found. Intermediate and weak pod forms of tunicate occur not only in prehistoric corn but also in living varieties. Varieties with elongated shanks, prominent leaf blades on the husks, and partly naked ears are common in South America. Varieties breeding true for branched ears are known in both South and Central America. Varieties in which the

development of secondary pistillate florets is the rule rather than the exception are well-known. Individual plants with mixed staminate and pistillate inflorescences are common in many varieties, especially in South America. There is apparently not a single condition intermediate between the hypothetical wild pod corn and modern, highly domesticated corn which does not still exist, usually somewhere in South America. The last fact, incidentally, is of special significance in supporting the hypothesis of a South American origin of maize.

DISCUSSION

Alphonse de Candolle in his classic "Origin of Cultivated Plants" emphasized the importance of utilizing all the evidence which can be brought to bear upon the problem involved in the origin of any particular cultivated plant and pointed out that even a combination of evidence can usually do no more than to lead to a strong probability that any given solution is correct. His conclusions regarding cultivated plants in general are particularly relevant with respect to the problem of the origin of maize, for unless maize should still be discovered actually growing in the wild, a possibility not yet ruled out, the problem of its origin may never be completely and finally solved. It may be possible, however, to accumulate a body of circumstantial evidence bearing upon the problem which will involve probabbilities that approach certainty. This point perhaps has not yet been reached. On the other hand, each year of additional research yields new evidence which increases the probabilities that the pod-corn hypothesis is valid and correct and strengthens the view that maize had its origin in South America from a wild form of pod corn. The least that can be said is that the pod-corn hypothesis is no longer merely a plausible alternative to the questionable teosinte hypothesis; it has now become a valid hypothesis in its own right with an impressive body of evidence to support it. The new evidence presented in this paper, that there exists a series of alleles intermediate between *Tu* and *tu*, that intermediate and weak forms of pod corn occurred not only in prehistoric corn, but are common in living varieties of South and Central America, is perhaps the most convincing evidence in support of the pod-corn hypothesis which has yet been brought forward. Considered in the light of the evidence, old and new, summarized in this paper, it appears to me to be conclusive, at least to the extent that the burden of proof now rests upon those who question the pod-corn hypothesis or favor any alternative to it. Indeed, I feel that with the evidence now at hand we can reconstruct the ancestral form of corn with at least as much confidence in the validity of our reconstruction as paleontologists have in their reconstruction of ancestral forms of man, the horse, and other animals.

SUMMARY

1. The *Tu* gene involved in pod corn causes, in appropriate conditions, the development of (a) prominent glumes, (b) pistillate spikelets in the tassel, (c) secondary pistillate florets, (d) branching of the pistillate inflorescence, (e) elongation of the rachis, (f) elongation of the branch supporting the ear.

2. All of these effects contribute to restoring a combination of characteristics probably once primitive.

3. Two spontaneous mutations at the *Tu* locus have occurred in the course of these studies, one from *Tu* to tu^h, the other from *Tu* to *tu*. In addition, an experiment on mutability of tu^h has yielded one mutation to *tu* in a population of 2125. This corresponds to a mutation rate of 471 per million gametes.

4. A weak form of pod corn called "half-tunicate" resulting from an intermediate allele, tu^h, at the *Tu-tu* locus shows 30 per cent of crossing over with *Su* on chromosome 4.

5. Still weaker alleles of *Tu* identified by linkage and other genetic tests are common in living varieties of maize. These have their highest frequency in the maize varieties of South and Central America, and their lowest frequency in inbred strains of the United States Corn-Belt.

6. Much of the prehistoric corn of Peru and some of the prehistoric corn of the American Southwest is identical in appearance to the weak pod corn of present-day Latin American varieties and undoubtedly represents a weak form of pod corn.

7. On the assumption that maize originated from a wild form of pod corn, a reconstructed ancestral form of maize would resemble *Tripsacum* in having lateral branches arising from the nodes of the stem and terminating in panicle-spikes which bear staminate and pistillate spikelets. It would differ from *Tripsacum* in annual habit, in possessing membranaceous rather than indurated glumes, in having a central spike, and in bearing paired pistillate spikelets.

8. Forms intermediate between this hypothetical ancestral form and present-day maize varieties are common in South America.

9. The early stages of the evolution of maize under domestication, those which occurred before *Tripsacum* entered the picture, are now visualized as a series of mutations at the *Tu-tu* locus, each producing numerous morphological changes which, when advantageous under domestication, were accentuated by selection, both artificial and natural, acting upon the modifier complex.

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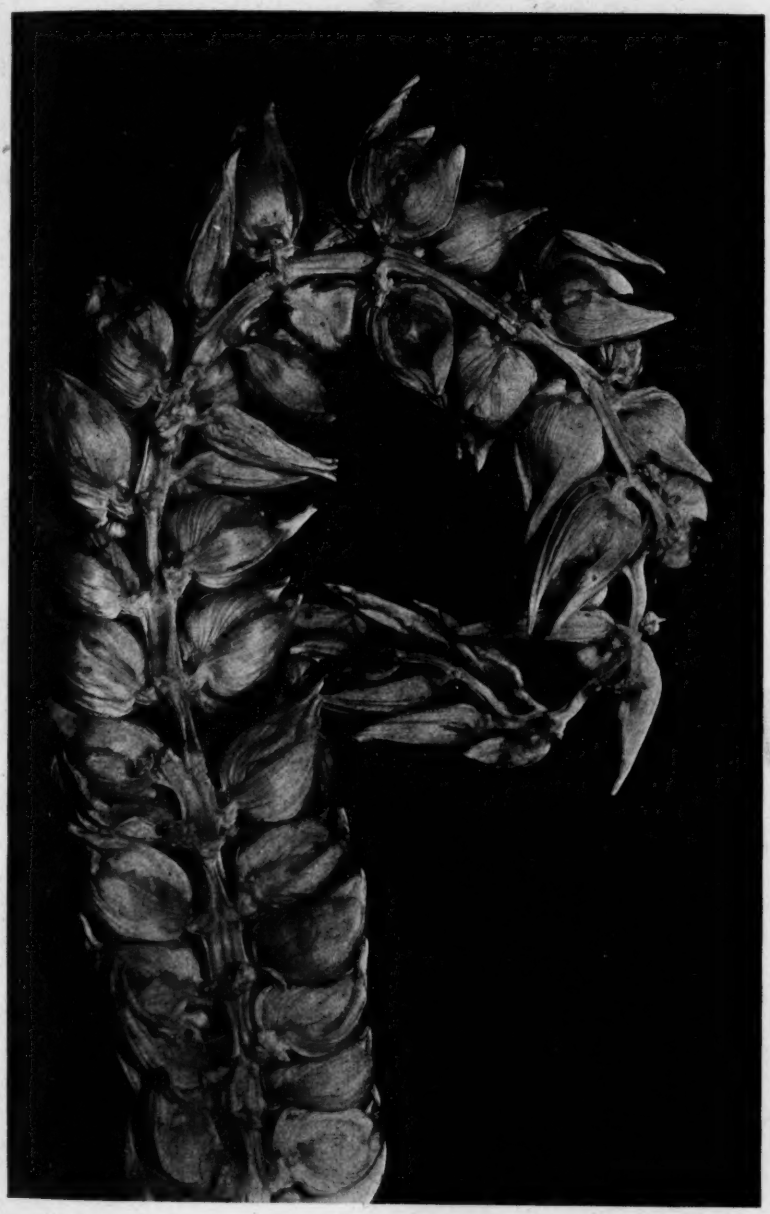
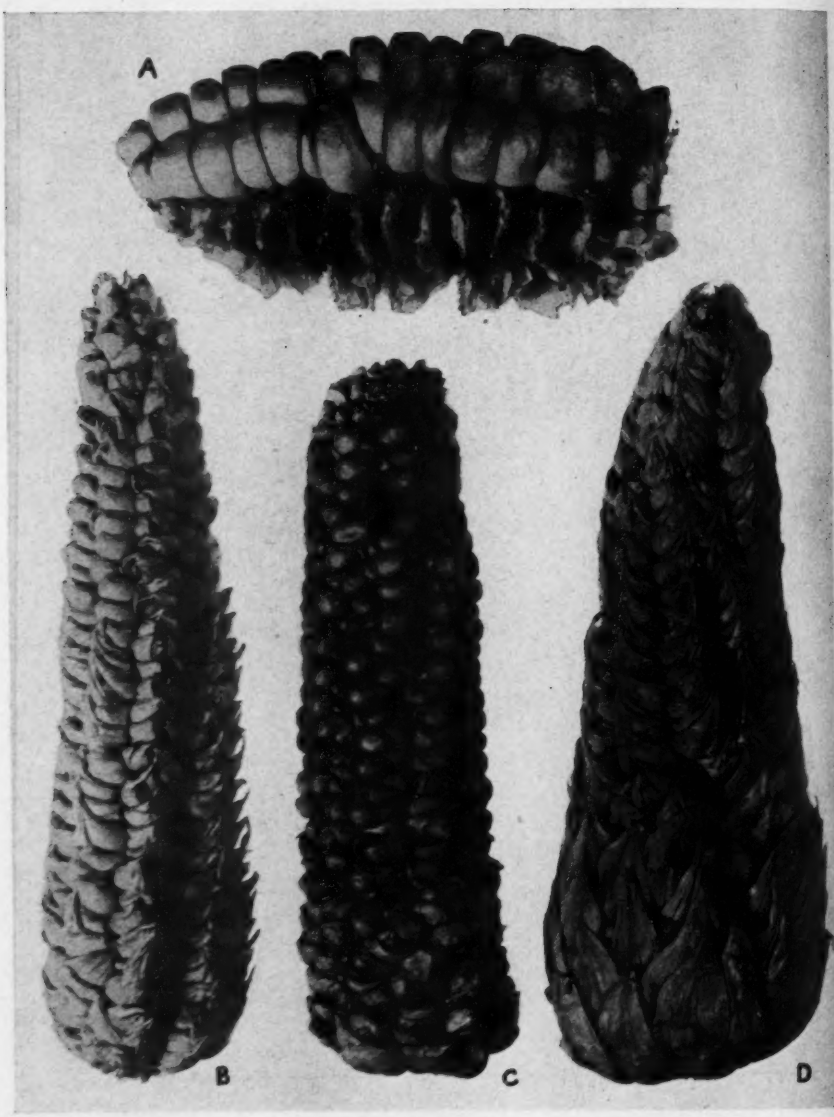
Explanation of Plate

PLATE 42

Terminal part of an ear of pod corn produced by crossing the Guarany maize of Paraguay by pod corn and backcrossing repeatedly to the Guarany parent. This ear illustrates several important characteristics of pod corn: (a) the glume-covered caryopsis; (b) the slender and fragile rachis; (c) the lack of compaction.



MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

Explanation of Plate

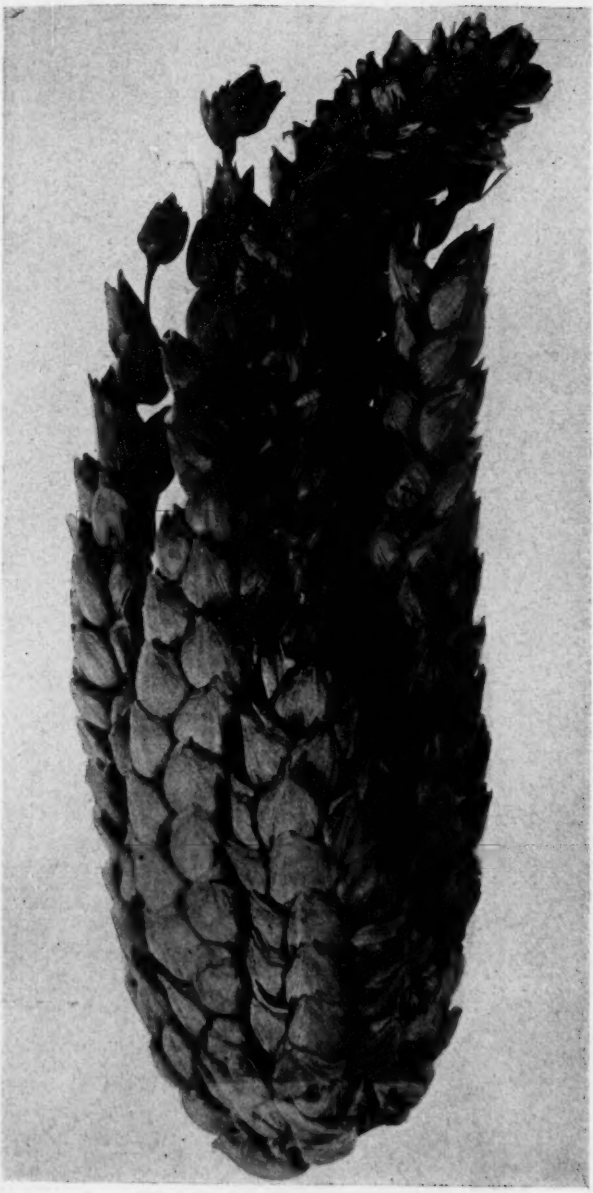
PLATE 43

Pod corn is still well-known in South America. Ears from three countries are illustrated in this photograph. A, Peru. B and C, Bolivia. D, Brazil.

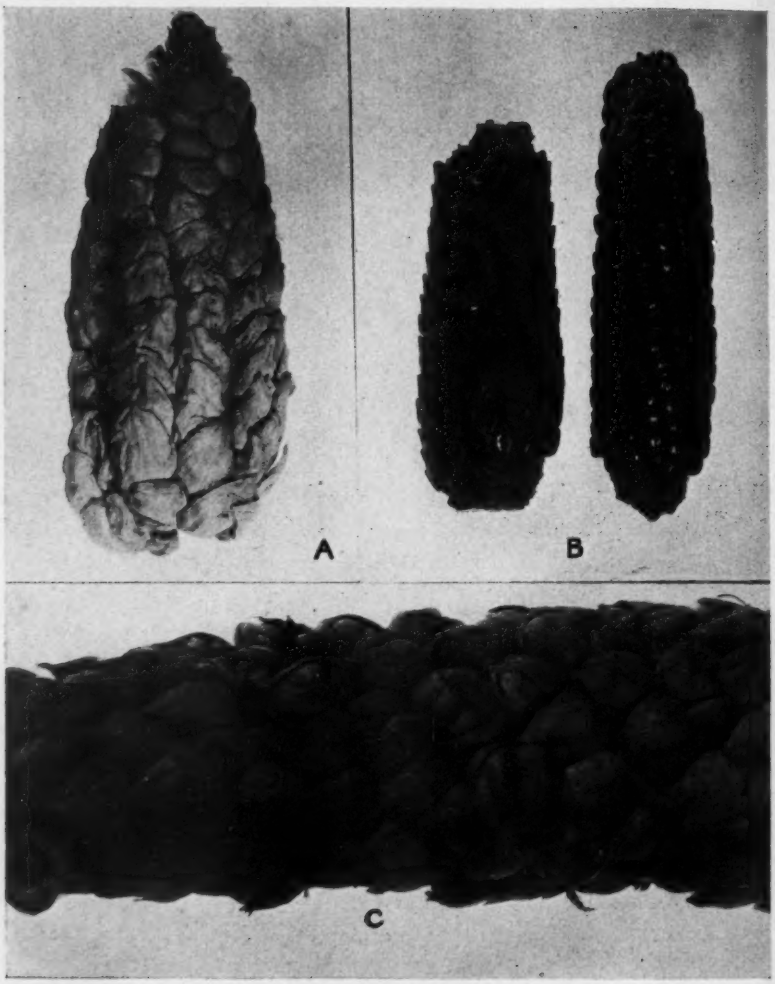
Explanation of Plate

PLATE 44

A branched ear of Guarany pod corn. It is not uncommon for ears of pod corn to be branched and this probably represents reversion to a primitive condition.



MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

Explanation of Plate

PLATE 45

A. Chimera which represents a mutation from *Tu* to *tu* in somatic tissue. B. Prehistoric ears from Paracas, Peru, showing "pockets" on surface of cob, characteristic of weak pod corn. C. Portion of an ear of Guarany pod corn showing double pistillate florets, possibly a primitive condition.

Explanation of Plate

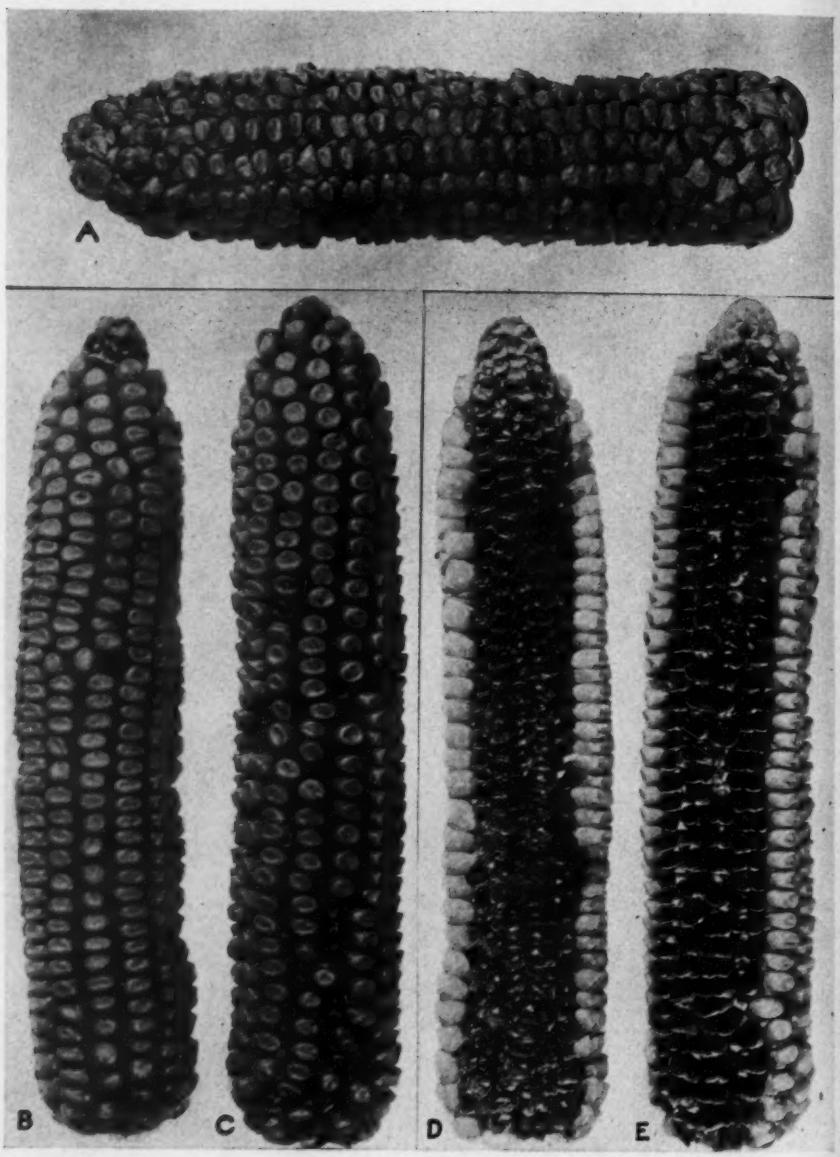
PLATE 46

A. An immature spike of tunicate teosinte showing the effect of *Tu* on the teosinte spike

B. Mature fruits from a similar spike. Note that the caryopses are completely enclosed in the glumes and that the rachis segments have become mere appendages.

C. Mature fruits of a variety of teosinte. Note that fruit cases comprise not only the glumes but also the rachis segments.

MANGELSDORF—POD CORN



MANGELSDORF—POD CORN

Explanation of Plate

PLATE 47

Ears from a relatively isogenic stock resulting from crossing and backcrossing to A158. A. An ear homozygous for tu^h. B and D. Two views of an ear homozygous for *tu*. C and E. Two views of an ear heterozygous for tu^h. Note that C which is heterozygous for half-tunicate is scarcely distinguishable from B, which is non-tunicate, until kernels are removed as in D and E. Note the alveolate surface of the cobs and the conspicuous pockets in E.

Explanation of Plate

PLATE 48

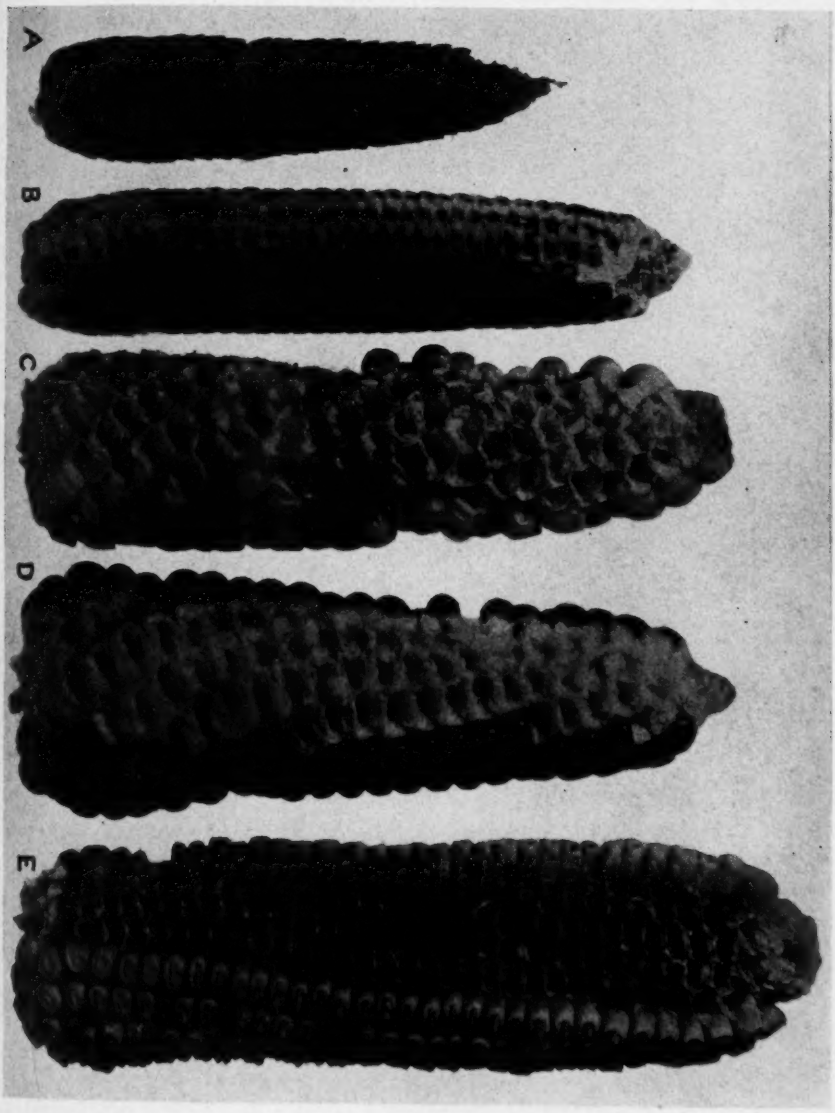
Maize varieties characterized by cobs with alveolate surfaces and conspicuous pockets and therefore probably weak pod corn.

A. Prehistoric ear from Nazca, Peru.

B. "Chapalote" maize from Mexico.

C and D. Similar ears from Colombia and Mexico, respectively.

E. An ear heterozygous for half-tunicate and therefore known to be a weak form of pod corn. Compare with ears A–D.



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